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- Articles dealing with any phase of botany relating to the Upper Great Lakes Region may be sent to the editor in chief. In preparing manuscripts, authors are requested to follow our style and the suggestions in "Information for Authors" (Vol. 15, p. 238).

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SOME MICHIGAN UPPER PENINSULA BIG TREES AND THEIR AGE ESTIMATES, ||

James R. Wells, Paul W. Thompson, and Gregory P. Fons

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In an earlier report (Wells & Thompson, 1981) we listed 43 trees from the Lower Peninsula of Michigan and suggested age for each. We described a design of an extractor for removing the increment coring bit which sometimes gets lodged in a tree. It is interesting to note that our extractor, if available, could have precluded the necessity of cutting down the world's oldest known living organism, a bristlecone pine (*Pinus aristata*), in order to remove the core sampler which had become lodged (Hitch, 1982).

This study is offered by way of complementing the former report but deals with Upper Peninsula localities where climatic regimes may be quite different, with a growing season up to four weeks shorter than in lower Michigan. (USDA, 1941). Interest in size-age correlation of northern trees is not a topic of only recent interest. Northern hardwoods forests were so studied more than 50 years ago (Gates & Nichols, 1930). While the present



Fig. 1. Author Gregory Fons taking increment core from black cherry tree in Alger County (collection no. 83). White pine stump at left had a diameter of 137 cm (54 in.).

study along with our 1981 report provides some range of possible ages of many species of the largest trees throughout Michigan, it is hoped that this work may stimulate other efforts at refining age estimation within a given

species as well as over a wider range of species distribution.

Field work was carried out during July 1981 and August 1982. Our collections (Table 1) numbered 1 through 67 were made during 1981 and those numbered 68 and following in 1982. Although collection sites are scattered over the Upper Peninsula, the predominance of Marquette County collections is due to the availability of large tracts of mature forests at the Huron Mountain Club property located some 27 miles (43 km) north of Marquette along Lake Superior's south shore.

Our methods are essentially those reported earlier (Wells & Thompson, 1981). We find, however, that with diffuse porous species and in other samples where growth ring visualization is difficult sanding the core samples (220 grit paper) usually renders them easy to count without staining (Susan

Matthews, pers. comm.).

In our earlier work we discussed some problems relative to growth ring counts as estimates of tree ages. In addition we refer the reader to collection nos. 47a & 47b, both taken from the same white cedar (Thuja occidentalis) at the same height $(4\frac{1}{2} \text{ ft.} = 1.4 \text{ m})$. The tree was leaning from a steep slope toward a ravine. The compression wood (i.e., the ring segments closest to the ravine) produced results leading to an age estimate of 326 years (47a). Another core segment of approximately equal length (no. 47b) taken 180° away, (i.e., up-slope on the opposite side of the stem), resulted in an estimate of only 265 years—a 27% lower estimate!

How old are the oldest trees in Michigan? Frequently, the oldest (and largest) trees are hollow or decayed in the center necessitating the extrapolation of age estimates from core segments somewhat less than a full radial length. However, using such abbreviated segments of a radial core we arrive at age estimates of approximately 650 years for white pine (Pinus strobus), red pine (Pinus resinosa), and white cedar (Thuja occidentalis). These estimates are based on collections nos. 25, 1, and 11, respectively. These three trees were found among virgin stands of timber on the Huron Mountain Club property and are more than double the age estimates of any tree we sampled from the Lower Peninsula. Approximately 20 years ago one of us (PWT) counted 530 growth rings on a white cedar on Leelanau County's Manitou Island, Lower Peninsula. This tree was reportedly blown down in 1910. Even larger living trees yet remain in this locality. Thus, it is probable that trees well over 600 years exist in this island locality and protected mainland sites on the Lower Peninsula could harbor giants of similar age. While older trees may exist in the Upper Peninsula, we believe they are to be expected in mature stands where some protection is afforded by topography or other large trees. It is interesting that these oldest estimates are from conifers. In addition, hemlock (Tsuga canadensis) can be as old as 469 years (collection no. 4), considerably more than the oldest deciduous species estimates, for sugar maple (Acer saccharum), no. 18, and white birch (Betula papyrifera), no. 69, whose age estimates were 364 yrs. and 352 yrs., respectively.

TABLE 1. Tree measurements and estimated age of selected Michigan upper peninsula large trees. Tree height and spread are listed in feet (meters); other measurements are in inches (cm); girth measurements were made at 4.5 ft.(1.4 m) above ground.

	Collection Number	County	Height	Crown	Girth	Diameter	Increment Core Length	Core Length Counted	Rings Counted	Estimated Age
Abies balsamea	20	Marquette	27	30	70.1	22.3	3.0	3.0	47	173
(Daisain III)	24	Marquette	69	33	50.6	16.1	2.8	2.8	38	108
			(21)	()	(128.5)	(40.9)	(7.2)	(7.2)		
	28	Marquette	85	29	58.3	18.6	9.7	7.5	99	82
			(56)	6)	(148.0)	(47.1)	(24.5)	(19.0)		
	40	Marquette	82	30	67.4	21.5	9.9	0.9	42	75
			(25)	6)	(171.2)	(54.5)	(1617)	(15.3)		
	9	Marquette	88	28	62.7	20.0	9.7	9.7	89	71
			(27)	6)	(159.3)	(50.7)	(24.5)	(24.5)		
Acer pensylvanicum	5	Marquette	99	32	30.4	7.6	8.3	3.9	41	52
(striped maple)			(11)	(10)	(77.3)	(24.6)	(21.1)	(8.8)		
	41	Marquette	59	30	24.0	7.6	6.9	3.8	42	42
			(18)	(6)	(6.09)	(19.4)	(17.5)	(6.7)		
	74	Marquette	33	23	22.5	7.2	5.4	3.2	09	29
			(10)	<u>(</u>	(57.1)	(18.2)	(13.7)	(8.1)		
	92	Marquette	49	56	28.8	9.2	5.8	4.3	20	53
			(15)	(8)	(73.2)	(23.3)	(14.8)	(11.0)		
Acer rubrum	42	Marquette	85	52	78.7	25.1	14.1	9.8	113	164
(red maple)			(56)	(16)	(199.8)	(63.6)	(35.8)	(21.9)		
	98	Alger	69	36	41.5	13.2	9.3	5.6	109	130
			(21)	(11)	(105.5)	(33.6)	(23.6)	(14.1)		
Acer saccharum	16	Marquette	138	84	95.0	30.2	12.3	12.0	272	342
(sugar maple)			(42)	(56)	(241.0)	(76.7)	(31.3)	(30.5)		
	18	Marquette	125	73	82.8	27.3	5.5	5.0	132	364
			(38)	(22)	(217.7)	(69.3)	(14.0)	(12.6)		
	80	Marquette	131	59	178.5	33.6	14.2	13.3	166	210
			(40)	(18)	(267.8)	(85.3)	(36.0)	(33.8)		
Acer spicatum	19	Gogebic	46	56	13.8	4.4	3.7	1.5	52	75
(mountain maple)			(14)	(8)	(34.9)	(11.1)	(9.3)	(3.9)		

TABLE 1. (Continued)

	Collection Number	County	Height	Crown Spread	Girth	Diameter	Increment Core Length	Core Length Counted	Rings Counted	Estimated Age
	65	Delta	30	29	12.5	4.0	3.0	2.0	15	15
			(6)	6)	(31.7)	(10.1)	(7.7)	(5.1)		
Betula alleghaniensis	34	Marquette	82	52	68.4	21.8	12.9	7.6	160	181
(yellow birch)			(25)	(16)	(173.7)	(55.3)	(32.7)	(24.5)		
	37	Marquette	82	55	62.3	19.9	11.3	6.9	91	130
			(25)	(17)	(158.3)	(50.4)	(28.6)	(17.6)		
	56	Ontonagon	79	50	70.9	22.6	12.8	10.9	106	110
)	(24)	(15)	(180.0)	(57.3)	(32.4)	(27.7)		
etula papyrifera	23	Marquette	92	52	6.69	22.3	12.9	8.8	109	138
(white birch)			(28)	(16)	(177.5)	(56.5)	(32.7)	(22.3)		
	69	Marquette	10	59	94.6	30.1	14.1	12.8	298	352
			(33)	(18)	(240.2)	(76.5)	(35.8)	(32.4)		
Fagus grandifolia	84	Alger	75	46	68.3	21.8	11.1	9.6	106	120
(beech)			(23)	(14)	(173.6)	(55.3)	(28.1)	(24.5)		
	85	Alger	59	43	46.1	14.7	7.7	7.5	88	87
			(18)	(13)	(117.1)	(37.3)	(19.5)	(19.0)		
Fraxinus nigra	45	Marquette	68	55	67.1	21.4	11.4	10.3	115	119
(black ash)			(27)	(17)	(170.3)	(54.2)	(29.0)	(26.2)		
	46	Marquette	92	55	58.5	18.6	13.3	7.1	89	68
			(58)	(17)	(148.6)	(47.3)	(33.8)	(18.0)		
Larix laricina	62	Gogebic	72	31	44.7	14.2	6.6	5.9	51	. 51
(tamarack)			(22)	(10)	(113.4)	(36.1)	(25.0)	(15.1)		
	87	Alger	69	56	45.0	13.4	10.0	5.0	58	78
			(21)	8	(106.7)	(34.0)	(25.5)	(12.7)		
	88	Alger	99	56	40.8	13.0	10.4	5.8	40	45
			(17)	(8)	(103.6)	(33.0)	(26.3)	(14.7)		
Ostrya virginiana	73	Marquette	99	33	32.3	9.01	9.2	4.8	130	145
(hop hornbeam)			(20)	(10)	(84.5)	(56.9)	(23.3)	(12.1)		
	81	Marquette	59	36	42.4	13.5	8.1	5.8	147	170
			(18)	(11)	(107.7)	(34.3)	(20.7)	(14.8)		
Picea glauca	∞	Marquette	103	56	103.2	32.9	14.0	14.0	137	161
(white spruce)			(31)	(8)	(262.0)	(83.4)	(35.5)	(35.5)		
	6	Marquette	79	23	62.5	19.9	7.6	7.6	78	102
			(24)	0	(158.7)	(50.5)	(19.3)	(19.3)		

54	5	63	122		114	132		121		117	101	10/	100		127		652		99		329		324		634		221		222		175		426	
54	i,	22	06		114	116		122		85	Ç.	0/	83	;	100		274		2		326		293		174		119		206		134		230	
13.4	(34.0)	(33.6)	6.9	(17.4)	0.7	4.7	(11.9)	5.3	(13.5)	7.1	(18.1)	0.3	5.4	(13.7)	11.5	(29.2)	7.4	(18.7)	12.7	(32.2)	15.4	(39.0)	16.8	(42.6)	8.3	(21.0)	14.3	(36.2)	18.8	(47.8)	14.3	(36.4)	12.3	(31.2)
15.3	(38.8)	(38.9)	13.1	(33.2)	8.3	9.3	(23.5)	9.5	(24.0)	11.8	(30.0)	10.0	11.2	(28.4)	15.0	(38.0)	7.4	(18.7)	12.7	(32.2)	22.7	(57.5)	21.2	(53.9)	8.3	(21.0)	20.8	(52.7)	21.0	(53.4)	14.3	(36.4)	15.8	(40.0)
26.5	(6/.3)	30.3	18.6	(47.2)	13.9	10.6	(26.9)	10.5	(26.7)	19.5	(49.5)	(36.5)	13.0	(33.0)	29.2	(74.0)	35.1	(89.0)	26.4	(6.99)	31.0	(78.7)	37.1	(94.1)	60.2	(152.9)	52.9	(134.3)	40.6	(103.0)	37.5	(95.2)	45.5	(115.5)
83.3	(211.4)	(241.3)	58.4	(148.3)	43.8	33.3	(84.5)	33.1	(83.9)	61.3	(155.5)	43.2	40.9	(103.7)	91.6	(232.5)	110.2	(279.6)	82.8	(210.2)	97.4	(247.2)	116.5	(295.6)	189.1	(480.4)	166.2	(421.9)	127.5	(323.6)	117.8	(299.1)	143.0	(362.9)
39	(12)	(14)	27	€ 8	9) <u>8</u>	(9)	15	(5)	35	<u>=</u>	75	26	8	20	(15)	19	(19)	40	(12)	99	(20)	74	(23)	99	(20)	28	(18)	47	(14)	34	(10)	42	(13)
08	(24)	(29)	86	(30)	76	2 2 2	(16)	62	(19)	69	(21)	90	99	(20)	85	(56)	06	(27)	79	(24)	75	(23)	151	(46)	135	(41)	174	(53)	141	(43)	115	(35)	112	(34)
Marquette	7.	Marquette	Ontonagon		Marquette	Marquette		Marquette		Marquette		Marquette	Marquette	1	Marquette		Marquette		Marquette		Marquette		Gogebic		Marquette		Marquette		Marquette		Keewenaw		Keewenaw	
29	6	39	59	20	2	14		15		22	5	5	4		50		_		26		46		2		25		31		48		53		54	

Picea mariana
(black spruce)
Pinus banksiana
(jack pine)

Pinus resinosa (red pine)
Pinus strobus (white pine)

TABLE 1. (Continued)

- 6 - 6 0 6 9 8 4 9
(15.6) 17.7 (45.0) 11.0 (28.0) 10.6 (26.8)
(45. 17. 10. 10. 12. 12. 12. 13. 14. 15. 15. 15. 15. 15. 15. 15. 15. 15. 15
(45. (28. 10. (26.
(30.4) 10.6 (27.0) 14.0
46.9 119.0) 29.9
147.3 46 (373.9) (119 (93.9 29
93.9
(14)

	71	Marquette	36	23	23.5	7.5	6.1	3.7	93	95
	12	Money	(11)	(C)	(59.7)	(19.0)	(15.6)	(9.3)	5	0
	7/	Marquette	(16)	10	(46.5)	7.7	2.9	C.I. (9.6)	/9	158
Thuja occidentalis	10	Marquette	82	19	8.96	30.8	4.0	4.0	80	307
(white cedar)	y-0	Marquette	(25)	9 ⁷	(245.7)	33.4	(10.2)	(10.2)	170	229
		anaph mit	(23)	; E	(267.0)	(85.0)	(11.4)	(11.0)	0/1	
	12	Marquette	79	30	83.2	26.5	10.6	10.6	184	231
	12	Moramotto	(24)	6) &	(2111.1)	(67.2)	(26.8)	(26.8)	130	154
	CI	Maidneile	(50)	66	(186.0)	(59.2)	(33.1)	10.4 (26.5)	138	154
	47a	Marquette	72	,04	85.3	27.1	7.4	6.3	150	323
		•	(22)	(12)	(216.4)	(68.9)	(18.8)	(16.0)		
	47b	Marquette	(same tre	ee as No.	. 47a)		7.1	7.1	138	265
							(18.0)	(18.0)		
Tilia americana	3	Marquette	105	62	144.0	45.8	6.9	2.9	98	288
(basswood)			(32)	(19)	(365.4)	(116.3)	(17.4)	(17.4)		
	17	Marquette	135	46	140	44.6	7.8	7.2	77	237
			(41)	(14)	(355.3)	(113.1)	(19.7)	(18.4)		
	19	Marquette	121	64	105.7	33.6	6.9	8.9	63	156
			(37)	(61)	(268.3)	(85.4)	(17.6)	(17.2)		
	79	Marquette	85	62	84.6	26.9	17.4	10.9	75	92
			(56)	(19)	(214.8)	(68.4)	(44.2)	(27.8)		
Isuga canadensis	7	Marquette	112	52	136.2	43.4	13.2	13.2	199	328
(hemlock)			(34)	(16)	(345.9)	(110.1)	(33.4)	(33.4)		
	4	Marquette	116	46	119.6	38.1	4.0	4.0	66	469
			(35)	(14)	(303.5)	(9.96)	(10.2)	(10.2)		
	36	Marquette	75	54	0.6	2.9	14.7	12.7	198	224
			(23)	(16)	(22.9)	(7.3)	(37.4)	(32.3)		
	55	Ontonagon	105	47	6.76	31.2	10.5	10.2	166	255
			(32)	(14)	(248.5)	(79.1)	(26.7)	(25.8)		
	77	Marquette	141	46	105.4	33.6	16.2	13.5	592	330
			(43)	(14)	(267.8)	(85.3)	(41.2)	(34.4)		
Ulmus americana	38	Marquette	95	98	118.2	37.6	16.1	13.9	118	160
(American elm)			(53)	(56)	(300.0)	(95.5)	(40.8)	(35.2)		
Viburnum opulus	29	Schoolcraft	23	13	7.6	2.4	1.9	1.2	12	12
(highbush-cranberry)			<u>(</u>	(4)	(19.2)	(6.1)	(4.7)	(3.1)		

Although highbush-cranberry (*Viburnum opulus*) and red-berried elder (*Sambucus pubens*) are commonly considered as shrubs, a sample of each is listed in Table 1 since both are included in a recent treatment on Michigan trees (Barnes & Wagner, 1981), and an unusually large specimen of each was located. The single age estimates are 12 yrs. for the highbush-cranberry (no. 67) and 17 yrs. for the red-berried elder (no. 35).

Large specimens of typically northern understory tree species such as striped maple (*Acer pennsylvanicum*) and mountain maple (*A. spicatum*) may be no more than 75 yrs. in age yet among the largest examples known.

The northern ranges of distribution of beech (Fagus grandifolia) and black cherry (Prunus serotina) include only portions of the Upper Peninsula (Little, 1971). Comparisons of size-age values for such species with tree data from the Lower Peninsula should take into account not only the Upper Peninsula's growing season, which depending upon specific sites may be shorter, but also the biological limit of species distribution. Differences in size-age values for species more widely distributed in Michigan such as white pine, hemlock, and sugar maple would be expected to reflect to a greater degree the climatic and edaphic factors and to a lesser degree the genetic factors associated with ecological amplitude.

The authors gratefully acknowledge the Huron Mountain Wildlife Foundation for support of this project and further acknowledge the assistance of A. Bruce Spike in locating collection no. 50, a new national champion tree. Don Henson assisted us with localities of selected large trees, as did state and national area foresters. The Michigan Nature Association kindly provided the Keweenaw Co. specimens for study.

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SUMMERBY SWAMP, AN UNUSUAL PLANT COMMUNITY IN MACKINAC COUNTY, MICHIGAN /

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Summerby Swamp, about eight miles north of the Straits of Mackinac and near Moran (Fig. 1), has an unusual floristic composition. Mogens C. Nielsen visited there in June 1965 and collected a subarctic composite, *Erigeron hyssopifolius*, which had not been found in Michigan since its first collection in 1890 by Farwell in Keweenaw County (Beal & Wheeler, 1892). Edward G. Voss, Frederick and Roberta Case, and Peter Harley in June 1977 found *Empetrum nigrum* (black crowberry), which has an arctic, circumpolar range, as well as *Primula mistassinica* (bird's-eye primrose), *Pinguicula vulgaris* (common butterwort), and *Juniperus horizontalis* (creeping juniper), all with a predominantly lakeshore distribution in the Great Lakes region. This paper reports on a study conducted primarily during the summer of 1980 and giving particular consideration to species of boreal and lakeshore affinities.

Michigan's Upper Peninsula was periodically glaciated during the Pleistocene from ca. 1.5 ± 0.75 million years ago until 4000 years ago (Dorr & Eschman, 1970). The last glaciation, the Wisconsinan, retreated for the last time from northern Michigan following the Greatlakean [Valders] readvance. Lake Algonquin was formed at the southern edge of the retreating glacier (ca. 11,500–10,500 years ago; Futyma, 1981). Lake Algonquin (at 605 ft. above sea level) covered a large part of the Great Lakes region, including most of the eastern Upper Peninsula and the area now occupied by Summerby Swamp (Futyma, 1981). As the glacier retreated farther it uncovered an outlet for Lake Algonquin through North Bay, Ontario (ca. 9,500 years ago; Dorr & Eschman, 1970), and the low-level stage of Lakes Chippewa (230 ft. in the Lake Michigan basin) and Stanley (190 ft. in the Lake Huron basin) was formed. As the North Bay outlet rose due to crustal uplift, the lake levels also rose, and when the outlets at Chicago and the St. Clair River were reached, the Nipissing lake stage (605 ft., ca. 4000 years ago; Dorr & Eschman, 1970) was initiated. Crustal uplift has caused the Nipissing shoreline to rise to its current level of about 640 ft. in the Summerby Swamp region (Futyma, pers. communication). It seems likely that the shoreline in the Nipissing lake stage was very close to or even cut across what is now Summerby Swamp, which has a current elevation of 635-645 ft. above sea level. If so, parts of the swamp have been above water and available for vegetation since the stage of Lakes Chippewa and Stanley.

The vegetation of Summerby Swamp has apparently remained virtually unchanged since the 1920's. Celia Jankist moved to the upland area just west

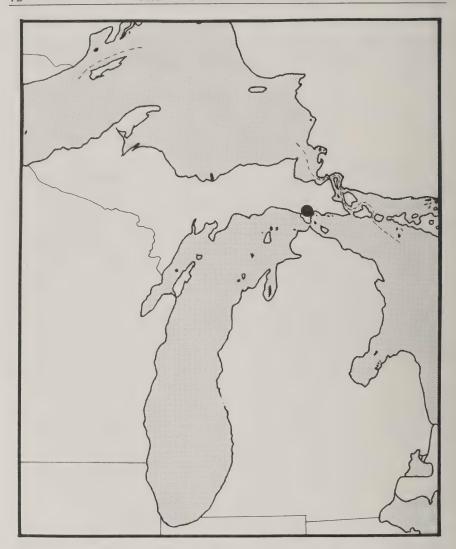


Fig. 1. Location of Summerby Swamp in northern Michigan.

of the swamp about 1922 soon after her father purchased a large portion of Summerby Swamp. She recalls that the swamp looked then as it does now, with the exception of a few corduroy roads put in by her father for removing logs from the east side of the swamp. Several such roads ran through Summerby Swamp but the vegetation almost covers them now.

The swamp is bordered on the east and west by bedrock limestone outcrop suggesting that there is limestone close to the surface of the swamp. This would explain the high pH of the water (7.5–8.0). Shallow streams of local origin running through the swamp join to form Summerby Creek which feeds into Hay Lake at the swamp's southern edge.



Fig. 2. A portion of Summerby Swamp with marly pools that resemble some shore areas of northern Lakes Michigan and Huron.

Most of the swamp, now part of the East Unit of Hiawatha National Forest, is a dense *Thuja occidentalis* (white-cedar) swamp. A small portion north of Highway M-123, hereafter referred to as Summerby fen (actually a rich fen-bog complex), has only sparse tree cover and contains marly pools which resemble some shore areas of northern Lakes Michigan and Huron (Fig. 2). Other portions of the fen resemble a Canadian muskeg. Table I lists the vascular flora of the fen. The terrain is flat, and the vegetation is low except for thickets of stunted *Thuja*, *Larix laricina* (tamarack), and *Picea mariana* (black spruce). Hummocks of *Sphagnum*, abundant on the marl substrate, permit acid-loving plants like *Chamaedaphne calyculata* (leatherleaf) and *Vaccinium oxycoccos* (cranberry) to grow beside such calciphiles

as *Potentilla fruticosa* (shrubby cinquefoil) and *Gentiana procera* (fringed gentian). Summerby fen is the southernmost known locality in Michigan for two boreal species, *Empetrum nigrum* (Fig. 3) and *Erigeron hyssopifolius* (Fig. 4).

Most of the species in Summerby fen are common in swamps and bogs throughout northern Michigan, but a few, Selaginella selaginoides, Pinguicula vulgaris, Primula mistassinica, Carex crawei, Juniperus horizontalis, Erigeron hyssopifolius, and Empetrum nigrum, are not. Three of these plants, Erigeron hyssopifolius, Pinguicula vulgaris, and Primula mistassinica, are common nearby in beach pools along Lakes Michigan and Huron, but rare inland this far south (Guire & Voss, 1963). At least one population of Pinguicula along the edge of a marly pool has been endangered by collecting or perhaps by hungry voles. (Plants observed in August 1980 had disappeared by October and conspicuous holes were left in the marly substrate.) Carex crawei is also common in the beach pool areas of Lakes Michigan and Huron and in rocky, calcareous areas east, west, and south of the Great Lakes but rare inland in the region (Guire & Voss, 1963). Juniperus horizontalis commonly grows on hummocks or in shallow water in Summerby fen. Elsewhere in the Great Lakes region it is characteristic of sand dunes. Northward it becomes more common in muskegs and similar inland habitats, but it is rare in such places as far south as Summerby fen.

Empetrum nigrum and Erigeron hyssopifolius grow vigorously in this locality. Thick mats of Empetrum cover numerous hummocks in the fen. E. G. Voss (pers. communication) reports that specimens collected in mid-June 1977 were covered with minute flowers, but when I visited the fen for the first time each season, on June 11, 1980 and May 17, 1981, Empetrum had finished flowering. In August 1980 it had set many fruits. Empetrum has been found in two white cedar-black spruce bogs in the Keweenaw Peninsula and also eastward along the shore of Lake Superior in the Pictured Rocks area at the summit of a cliff and on sandy banks and in Luce county near Deer Park, also on sandy banks. The distribution of Empetrum in the Lake Superior region has been mapped by Soper & Voss (1964). Erigeron hyssopifolius is very abundant in the fen and dots sunny spots with small white-rayed flower heads. It occurs elsewhere in North America along "rocky shores and banks, or occasionally on ledges and rocky places away from water, northern Vermont and New Hampshire, Maine, and southeastern Canada, and northwestward to Great Bear Lake, Mackenzie Territory' (Cronquist, 1947).

Three species found in Summerby fen, Erigeron hyssopifolius, Empetrum nigrum, and Pinguicula vulgaris, are listed as threatened in Michigan.

In the flora of Summerby Swamp south of Highway M-123, I found a similar array of habitats with most of the same species, notably *Primula mistassinica* and *Erigeron hyssopifolius*, but not *Empetrum nigrum*, *Pinguicula vulgaris*, and *Juniperus horizontalis*.

Other plants common to Summerby fen and the nearby beach pools include Castilleja coccinea, Drosera rotundifolia, Lobelia kalmii, Utricularia cornuta, and Aster ptarmicoides. Many northern mosses associated with beach pools in the Great Lakes region are present in Summerby Swamp:



Fig. 3. A small plant of Empetrum nigrum (height approx. 10 cm) growing in shade of Thuja occidentalis with Vaccinium oxycoccos and Carex aquatilis.



Fig. 4. Erigeron hyssopifolius in bloom in late June.

TABLE 1. Vascular Flora of Summerby fen in Summerby Swamp. Abundance: v—very abundant and widespread. a—abundant, freqently observed. l—locally abundant, observed in few localities. s—sparse, of local occurrence. r—rare, discovered only once or twice and with few individuals.

Equisetum arvense s Malaxis unifolia r E. variegatum s Salix rigida 1 E. scirpoides s S. candida 1 Myrica gale 1 Selaginella selaginoides s Abies balsamea s Comandra umbellata v Picea mariana v Geocaulon lividum r Larix laricina v Arceuthobium pusillum as Pinus strobus a Sarracenia purpurea v Drosera rotundifolia v Thuja occidentalis Juniperus communis r Parnassia glauca v J. horizontalis v Fragaria virginiana 1 Triglochin maritimum v Potentilla fruticosa v Rosa palustris s T. palustre v Phragmites australis 1 Polygala paucifolia s Deschampsia cespitosa 1 Empetrum nigrum 1 Calamagrostis canadensis s Rhamnus alnifolia a Muhlenbergia glomerata a Viola affinis 1 Panicum implicatum a V. conspersa 1 Eleocharis pauciflora a Shepherdia canadensis s E. elliptica a Pyrola asarifolia s Scirpus cespitosus v Ledum groenlandicum v S. hudsonianus v Kalmia polifolia a S. acutus a Andromeda glaucophylla a Eriophorum viridi-carinatum a Chamaedaphne calyculata v Rhynchospora capillacea s Epigaea repens 1 Gaultheria procumbens a Cladium mariscoides s Carex sterilis a G. hispidula 1 C. concinna r Gaylussacia baccata 1 C. eburnea s Vaccinium angustifolium s V. oxycoccos v C. aurea s Primula mistassinica 1 C. aquatilis v C. buxbaumii r Trientalis borealis 1 C. capillaris v Gentiana procera v C. crawei r Halenia deflexa s C. vaginata s Prunella vulgaris a C. flava 1 Castilleja coccinea s C. viridula 1 Melampyrum lineare s Juneus balticus a Utricularia cornuta 1 J. alpinus a Pinguicula vulgaris 1 Tofieldia glutinosa v Lonicera oblongifolia 1 Linnaea borealis a Zigadenus glaucus a Lilium philadelphicum s Valeriana uliginosa a Smilacina trifolia a Lobelia kalmii v Majanthemum canadense s Solidago uliginosa Iris versicolor s S. gigantea s Cypripedium calceolus a S. graminifolia s Habenaria viridis r Aster simplex s A. ptarmicoides v H. hyperborea s Calopogon tuberosus a Erigeron hyssopifolius v Arethusa bulbosa r Petasites palmatus 1 Spiranthes romanzoffiana s Senecio pauperculus a

Scorpidum scorpioides, Castoscopium nigritum, Hypnum pratense, Distichium inclinatum, Drepanocladus vernicosus, Campylium stellatum, and Sphagnum warnstorfii. A rare northern moss, Tetraplodon angustatus was discovered by Virginia Streusand in the swamp in June 1980. It has been reported from Maine, New Hampshire, New York, Michigan, and various parts of Canada.

Plants occurring in Summerby fen and common along the rocky shores of Lake Superior include *Pinguicula vulgaris*, *Primula mistassinica*, *Selaginella selaginoides*, *Drosera rotundifolia*, *Ledum groenlandicum*, *Kalmia polifolia*, *Aster ptarmicoides*, *Erigeron hyssopifolius*, *Empetrum nigrum*, *Scirpus cespitosus*, and *Potentilla fruticosa*. Species common to inland muskegs north of Lake Superior and Summerby fen, include *Empetrum nigrum*, *Scirpus cespitosus*, *S. hudsonianus*, *Selaginella selaginoides*, *Drosera rotundifolia*, *Ledum groenlandicum*, *Kalmia polifolia*, *Potentilla fruticosa*, and *Juniperus horizontalis*.

In summary, the area apparently was a Lake Nipissing shoreline. Because of a limestone substrate, it was quite calcareous and probably resembled the marly beach pools of the present Great Lakes. *Empetrum nigrum, Juniperus horizontalis, Pinguicula vulgaris, Primula mistassinica, Carex crawei, Erigeron hyssopifolius, Aster ptarmicoides, Selaginella selaginoides* and many other species probably thrived in this shoreline habitat. Because of a lack of disturbance, cold water, cold air drainage, and possibly other climatic factors, these plants have persisted here at least since the Nipissing lake stage, or perhaps since the stage of Lakes Chippewa and Stanley, about 9500 years ago.

A number of people assisted with field work and helpful comments: Heidi Van't Hof, Judith Gendlin, Virginia Streusand, Kim Jones, Nina Shishkoff, Michael Mayfield, Barbara Madsen, Conrad Istock, Edward G. Voss, and Stanley H. and Marilyn Weitzman. Dr. Voss, Heidi Van't Hof, Dr. Weitzman, Marilyn Weitzman, Robert J. O'Hara, Dr. Peter F. Stevens, Dr. Norton Miller, and Elizabeth A. K. Coombs offered helpful advice on the manuscript. An extra note of thanks is due to Dr. Voss for suggestions and support throughout this project which was completed as a senior honors thesis at the University of Michigan. I am grateful to the University of Michigan Biological Station for research facilities and the Honors Council for financial support.

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CINCLIDIUM STYGIUM, A MOSS NEW TO MINNESOTATI

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During the summer of 1982, Cinclidium stygium was collected in Koochiching County, northern Minnesota. The collections represent the first records for this state. Cinclidium is differentiated from related genera of the Mniaceae (Koponen 1974; Mogensen 1973) by an entire, well-developed leaf border, a single U-shaped, dorsal stereid band in the costa, macronemata in rows on the stem, and a unique peristome and capsule structure. Cinclidium stygium is distinguished by elliptic to obovate, sharply apiculate leaves with a well-developed costa that reaches the leaf apex; a unistratose border; and irregular, elongate, thick-walled leaf cells (Mogensen 1973). The plants are very distinctive because of the deep red of older leaves and an apiculus that is red even in young green leaves.

Cinclidium stygium is an indicator of rich fen conditions (Persson 1961). The collections of Pine Island State Forest grew in rich fen drains (open, very minerotrophic fen tracks in poor fen forest) and in association with rich fen species such as Scorpidium scorpioides, S. turgescens, Calliergon trifarium, Drepanocladus revolvens, Campylium stellatum, Bryum pseudotriquetrum, Paludella squarrosa, Moerckia hibernica, Hypnum lindbergii, Riccardia palmata, Fissidens adianthoides, and Tomenthypnum nitens. The water track was dominated by Scirpus validus, S. cespitosus var. callosus, Carex exilis, and C. lasiocarpa var. americana. Other prominent species included C. limosa, C. livida var. grayana, Eleocharis compressa, and Drosera anglica.

According to Mogensen (1973), Ireland et al. (1980) and Crum & Anderson (1981), Cinclidium stygium has a bipolar, circumboreal distribution in northern Fennoscandia (south to England, Poland, and central Germany), and Siberia, and from Alaska to Greenland and Iceland south to Saskatchewan, northern Michigan, and Anticosti Island and through the western mountains south to British Columbia and Alberta, and also in South America (in southern Argentina and Tierra del Fuego).

Koochiching County: Pine Island State Forest, 14 km E of Waskish and 2 km N of Tamarac River (48°12′00″N, 94°19′24″W, 365 m), Janssens 8866, 8881, 8902, 8929 (MIN).

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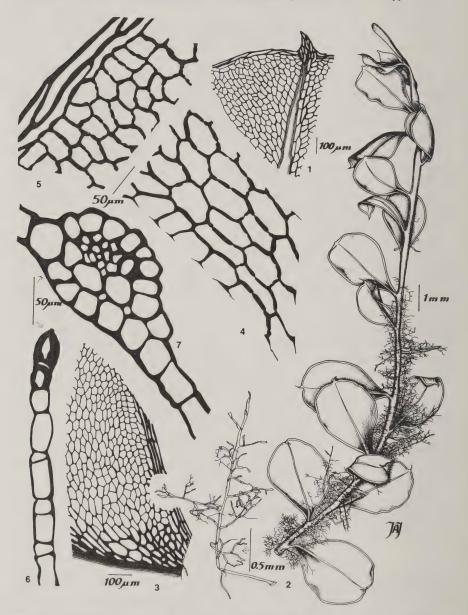
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Figs. 1–7. Cinclidium stygium Sw. (Janssens 8866 & 8881). 1. Leaf apex. 2. Plant and enlarged macronema. 3. Basal leaf cells. 4. Median cells. 5. Lamina and border. 6. Lamina and border in section. 7. Costa in section.

VEGETATIVE REPRODUCTION IN PLATYDICTYA []

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Platydictya jungermannioides is an exceedingly small moss rarely collected in the Great Lakes region, partly because of its tendency to occupy hideaway habitats. It has been collected a few times in wet calcareous habitats in northern Michigan, in Thuja swamps in hollows under the roots of trees (Emmet, Cheboygan, and Mackinac Counties) and once in moist crevices in a limestone sink (Alpena County.) Janice Glime, in an unpublished account of bryophytes of the Keweenaw Peninsula, records its occurrence in a basalt gorge at Jacob's Creek Falls. In more northern parts of the continent the plants often grow in mixture with mosses of densely tufted growth. The species is found in montane localities in the crevices of cliffs often under ledges, and on peaty soil of banks sheltered by overhang.

Because the plants are dioecious and commonly grow in shelter, the sexual cycle is not easily completed. In the herbarium of the University of Michigan I found only one fruiting collection (Drummond's *Musci Americani 190*, on shady banks among the Rocky Mountains). I found only one other collection with female inflorescences. Yet the species is widely distributed from Greenland to Alaska and south to New England, Michigan, Wisconsin, Colorado, Idaho, and Washington. It also occurs in northern and central Europe. (Records from northern Asia, Japan, California, Arizona, and New Mexico were not confirmed.)

The wide disperal of the species may result from minute brood bodies produced in leaf axils. By searching with high power of the microscope (×400), and with difficulty, I found gemmae from New Brunswick, Michigan (Alpena Co.), Colorado, Idaho, British Columbia, Bathurst Island, Devon Island, Finland, and Hungary. Correns, in *Die Vermehrung der Laubmoose*, illustrated gemmae from Austrian plants and reported that Loeske had searched his herbarium and found gemmae from only two localities. Nyholm in the *Moss Flora of Fennoscandia* characterized them as elongate; her illustrations, however, correctly show short, obcuneate bodies. Smith, in the *The Moss Flora of Britain and Ireland*, mentioned "axillary gemmae, 100–320 µm long." I have not seen gemmae of such length, but there is no question that the plants illustrated in Smith's flora are correctly named. The gemmae are accurately depicted in Ireland's *Moss Flora of the Maritime Provinces* (of eastern Canada).

The gemmae, 30–45 μm long and virtually colorless, occasionally occur in great numbers in radiating clusters, but more commonly only a few are produced and in only few of the leaf axils. They are 3-celled (or very rarely 4-celled). The basal cell is thin-walled; the upper cells are thickwalled, and the apical cell is adorned by three or four spreading papillae. According to Correns, the gemmae are cut off from a stalk cell by a short cell

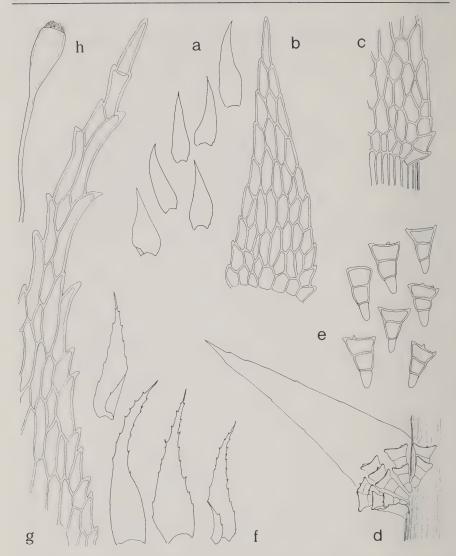


FIG. a–g. *Platydictya jungermannioides*. a. Branch leaves, $\times 80$. b. Branch leaf showing areolation, $\times 230$. c. Alar cells, $\times 230$. d. Axillary cluster of gemmae, $\times 230$. e. Gemmae, $\times 370$. f. Perichaetial leaves, $\times 80$. g. Apex of perichaetial leaf, $\times 370$. h. Capsule, moist, $\times 18$.

which he called a brachytmema (in contrast to a longer dolichotmema causing abscission in some other species). He reported good germination of gemmae from material dried as long as one month. It is the thin-walled basal cell that elongates and divides to form a protonema.

The species, though modest in size and appearance, is easily recognized by serrulate basal leaf margins, very few short alar cells, and spinose-dentate perichaetial leaves.

REPRODUCTIVE ECOLOGY OF FIVE HERBS COMMON IN CENTRAL ILLINOIS

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Breeding systems and patterns of fruit production were studied in central Illinois populations of Capsella bursa-pastoris, Melilotus officinalis, Penstemon digitalis, Polygonatum commutatum, and Smilacina racemosa. Capsella bursa-pastoris was autogamous; the others appeared to require pollinators. Observations on fruit set as well as data from hand-pollinations suggested that fruit production in C. bursa-pastoris, M. officinalis, P. digitalis, and S. racemosa was not pollinator limited. Populations of P. commutatum in the forest interior may have been pollinator limited, but those in open areas were not.

Relatively little is known about factors limiting fruit production in angiosperms (Lloyd 1979). Recent literature reviews (Stephenson 1981; Willson & Burley in press) suggest that fruit production is frequently resource limited, but in some species pollen availability limits reproduction (e.g., Bierzychudek 1981; Bertin 1982). Knowledge of the role of resources, pollen, or such factors as seed predation in limiting maternal investment in plants is required to determine the extent of sexual selection (Willson 1979; Charnov 1979) and understand the evolution of floral displays (Willson & Rathcke 1974; Willson & Price 1977; Janzen 1977).

Our objective was to examine the reproductive systems of five central Illinois herbs and assess the role of pollen in limiting fruit and seed production. We deliberately selected species with different life histories and from different habitats so as to broaden the implications of our study. We examined Capsella bursa-pastoris, a winter annual of disturbed areas; Melilotus officinalis, a biennial of disturbed areas; Penstemon digitalis, a perennial of old fields and prairies; and Polygonatum commutatum and Smilacina racemosa, both perennials of forests and open areas. For each species we attempted to determine the breeding system and whether seed production was limited by pollinators. The methods varied somewhat among species, as some lent themselves to approaches that were unsuitable for others.

CAPSELLA BURSA-PASTORIS was studied at Patterson Park, Urbana. The species is reported to be autogamous (Fryxell 1957), and we

¹Scientific contribution 1197 from the N. H. Agricultural Experiment Station. We thank the University of Illinois Research Board for partial financial support.

checked this designation by bagging 10 plants with dialysis tubing in May 1978. Bags were removed and fruit production recorded on May 29. To determine what proportions of flowers produced mature fruit, inflorescences from 15 unbagged plants were examined after fruit maturation was nearly completed. The numbers of flowers and mature fruit per inflorescence were counted.

For the ten inflorescences bagged, six bags were destroyed or removed by wind or rain. In the four remaining bagged inflorescences, all flowers (13–15) in three of the inflorescences resulted in mature fruits while, in the fourth, only three of 15 flowers failed to produce fruit. Thus it is evident that the plants did not require a pollinator (see also Fryxell 1957) and were thus not pollen limited. In the 15 inflorescences examined for flower and fruit production, the mean percentage of flowers producing fruit was 94.8. Most flowers failing to produce fruit were at the very tip of the raceme and thus were the last produced. The flowers were in the process of developing when the whole plant senesced, presumably due to time or resource limitation.

MELILOTUS OFFICINALIS was studied at Mayview Prairie, 11 km east of Urbana. On 16 June 1978, 30 inflorescences (containing 50–100 flowers each) on 30 different plants were marked. Ten were bagged with dialysis tubing and not manipulated; ten, unbagged, were visited daily to hand-pollinate open flowers with pollen from different plants in the same population; and ten were left as unbagged controls. The number of flowers and numbers of developing and mature fruits were recorded weekly until fruit maturation was complete.

The results of the bagging experiments suggest that M. officinalis requires a pollinator to produce fruit (as also observed by Fryxell 1957). Of the ten bagged inflorescences four were destroyed by wind or grasshoppers, and none of the other six produced fruit. Of the ten inflorescences left open to natural pollinators, one was destroyed, but the nine remaining inflorescences produced mature fruit. An average of 46% of the flowers in these inflorescences produced fruit. Similarly, in the ten inflorescences that were hand-pollinated in addition to natural pollination, 41% of the flowers resulted in mature fruit. The fecundities for manually pollinated and control inflorescences are not significantly different (Mann-Whitney U=59.5, P>0.05), suggesting that fruit production was not limited by pollinators.

PENSTEMON DIGITALIS was studied at the University of Illinois Ecological Research Area. The breeding system was examined by marking and bagging 40 flowers (on 40 different plants) with dialysis tubing on 7 June 1978. As flowers opened they were subjected to the following treatments: ten were left bagged and the flowers not manipulated to determine whether autogamy occurred; 15 were hand-pollinated with pollen from the same plant to determine self-compatibility; and 15 were hand-pollinated with pollen from a different plant. Bags were removed after flowering and fruit development was followed to maturation.

To test whether pollination limited fruit production, 20 inflorescences (with about ten flower buds each) on 20 different plants were randomly selected and marked on 7 June 1978. Ten of the inflorescences were not manipulated; the other ten were visited daily and open flowers were hand-

pollinated with pollen from a different plant. Hand-pollination was continued until all inflorescences were through flowering (around 25 June). Subsequent fruit development was followed to maturation.

The results of the breeding system experiments suggest that *Penstemon digitalis* requires a pollinator for fruit production but that the plants are self-compatible. Only one of ten bagged flowers produced fruit, while 53% of selfed and 58% of outcrossed flowers yielded fruit. The flowers remained open for two to three days and were strongly protandrous, with stigmas becoming receptive on the second or third day.

The results of hand-pollination suggest that fruit production was not pollen-limited. In control and experimental inflorescences the mean percentages of the flowers producing mature fruits were 85 and 87, respectively, and not significantly different (Mann-Whitney $U=53,\,P>0.05$). In most inflorescences flowers that did not develop fruit were the last to bloom. Most inflorescences also contained flower buds that did not open; these were located at the distal end of the raceme and were thus the last buds produced, suggesting that resources were insufficient to support further fruit production.

POLYGONATUM COMMUTATUM was studied between 5 June and 4 July 1978 in Trelease Woods, 6 km NE of Urbana. The breeding system was examined by marking and bagging 12 stems. On four of these, all open flowers were removed and unopened flowers were bagged and not manipulated to test for autogamy. On four others, flower buds were bagged and then pollinated with pollen from the same plant to test for self-compatibility; on the remaining four stems bagged, flowers were pollinated with pollen from other plants to test for cross-compatibility. Plants were checked on 4 July to determine fruit set.

Fruit set in plants on the sunlit edge of both Trelease Woods and Brownfield Woods (7 km NE of Urbana) was compared with that in the interiors. For 30 plants at the edge and 30 in the interior of each stand, the numbers of flowering nodes per stem (ramet), flowers per stem, and fruits set per stem were recorded. Fruit set on these same plants was assessed in Trelease Woods on June 21 and Brownfield Woods on July 3.

Field observations showed that anthers dehisced in the bud and that by the time the flower opened most of the pollen was already gone. The anthers were pressed up against the style in bud and at anthesis. The only insects visiting *Polygonatum* were bumblebees (*Bombus* sp.).

That only seven of the 80 (9%) bagged and unmanipulated flowers matured fruit suggests that this species generally requires a pollinator. The seven flowers producing fruit may have resulted from bees forcing buds open just before bagging. For both hand-selfed and outcrossed flowers, 46% set fruit, indicating self-compatibility.

The comparison between fruit set at the forest edge and in the forest interior showed that the number of flowering nodes per stem for edge and interior plants was similar at Trelease Woods but greater for edge plants at Brownfield Woods; that a greater number of flowers was produced and a greater proportion of these initiated fruits in edge microhabitats in both forests; and that a greater number of fruits was set per stem at the edges of

TABLE 1. A comparison of flowering nodes per stem, number of flowers produced on all stems, percent of flowers failing to set fruit, and number of fruits set per stem, in edge and interior populations of *Polygonatum commutatum* in Trelease and Brownfield Woods.

	Edge	Interior
Trelease Woods	(n = 30 plants)	(n = 30 plants)
# flowering nodes/stem	$\bar{x} = 9.2$ $SE_{\bar{x}} = .8$	$\bar{x} = 8.1$ $SE_{\bar{x}} = .6$
Total # of flowers	703	$5L_{\bar{x}} = .0$
% fl. failing to fruit	40%	79%
# fruit/stem	$\bar{x} = 14.0$	$\bar{x} = 3.6$
	$SE_{\bar{x}} = 2.3$	$SE_{\bar{x}} = 1.0$
Brownfield Woods	(n = 30 plants)	(n = 30 plants)
# flowering nodes/stem	$\bar{x} = 12.3$	$\bar{x} = 4.1$
	$SE_{\bar{x}} = .7$	$SE_{\bar{x}} = .4$
Total # of flowers	1133	20 4
% of fl. failing to fruit	55%	93%
# fruit/stem	$\bar{x} = 17.2$	$\bar{x} = .5$
	$SE_{\bar{x}} = 3.2$	$SE_{\bar{x}} = .25$

both forests than in the interior (Table 1). Thus, at Trelease, there was similar fruiting effort in both habitats, but the percentage of flower failure was much higher in the interior, with the number of fruits per stem correspondingly low. Reduced fruit set in the interior could be due to reduced pollinator activity or to light levels insufficient to mature many fruits. If the breeding system data are compared with those in Table 1, it is evident that manual pollination did not increase the percentage of flowers setting fruit over naturally pollinated plants at the edge of Trelease Woods (46% vs. 60%) but did so in the interior (46% vs. 31%), suggesting that fruit set in the interior is pollinator limited. Thus the occurrence of pollen limitation may be related to microhabitat conditions.

At Brownfield Woods, flowering effort was far larger at the edge, and flower failure was much higher in the interior. Thus, in this population but not in Trelease Woods, individual stems seemed to adjust their flowering effort to the local environment.

SMILACINA RACEMOSA populations were studied in three microhabitats in Trelease Woods: forest edge, light gaps, and forest interior. Pollinator observations totaling 18¾ hrs were made between 0600 and 2000 hrs on 25–30 May 1978. In each site the number of pollinator visits per stem was recorded. Flowering effort was assessed by counting the branches in the panicles of individual plants. Sample sizes were 23 plants on the edge, 12 in the gap, and 23 in the forest interior. Fruit set was assessed on 13 June and fruit maturation on 2 September 1978.

The most common visitors were flies, beetles, and (to a lesser extent) bees. Visitation rates were highest in the edge microhabitat (120 visits per hour per inflorescence), lowest in the interior (8), and intermediate in forest gaps (89). Thus, the greatest potential for pollinator limitation appeared to be in the forest interior.

Flowering effort, measured as the number of branches in the panicle on

each stem, was highest in the edge and gap microhabitats (21.1 and 20.5, respectively) and lowest in the interior (11.3). Thus, stems adjusted flowering effort according to habitat. Comparative fruit set on 13 June 1978 was 222 fruits per stem in the edge microhabitat, 151.5 in the gap microhabitat, and 45.6 in the interior. On 2 September, one of the edge plants was dead, 12 had no fruit ($\bar{x} = 4.2$ fruits/stem), four had normal fruit ($\bar{x} = 4.7$ fruits/stem), and one had 49 normal and 56 tiny fruits. The mean number of large and small fruits per stem on edge plants was 13.7. In the gaps, all stems died: in the interior, one had 20 fruits while the other 22 had died. That the number of mature fruits per stem was lower than the number of initiated fruits per stem in both edge and interior habitats suggests that fruit production was resource-limited in both habitats. According to Fryxell (1957), some populations of Smilacina are apomictic, and where this is true, it is certain that pollen does not limit reproduction. However, bagging experiments conducted by Willson (unpubl.) in the spring of 1981 indicate that apomixis does not occur in our populations.

DISCUSSION

Fruit production in *Penstemon, Melilotus, Smilacina*, and edge populations of *Polygonatum* was apparently not limited by pollinators. The data suggest that one of the important assumptions of sexual selection theory, resource limitation of reproduction (Willson 1979; Charnov 1979), may apply to these populations. That forest populations of *Polygonatum* were apparently pollen limited suggests that reproductive systems of populations in different microhabitats may be subjected to very different selection pressures. Pollen limitation of forest understory plants has also been reported elsewhere (e.g. Bierzychudek 1981).

All the species, except *Polygonatum*, initiated a greater number of fruits than were matured. Such over-initiation is common (Stephenson 1981; Willson & Burley in press) and may be favored evolutionarily by predation of young fruits, ability of the plants to selectively mature fruit, and environmental unpredictability during the period of fruit-filling (Janzen 1977; Stephenson 1981; Lee & Bazzaz 1982). It is not possible to test these hypotheses with our data, but in *Capsella* and *Penstemon* late-initiated flowers and fruit were the least likely to mature. This suggests that these plants were programmed to capitalize on extra resources or time, indicating that the environmental unpredictability hypothesis may be valid for these populations. The indeterminate inflorescences in these and many other species may thus be an adaptation to resource unpredictability, providing continuous fruit initiation as long as favorable conditions prevail.

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REVIEW

FERNS AND FERN ALLIES OF THE DRIFTLESS AREA OF ILLINOIS, IOWA, MINNESOTA, AND WISCONSIN. By James H. Peck. Milwaukee Public Museum Contributions in Biology & Geology No. 42. 140 pp. \$12.50.

This is an up-to-date treatment of the pteridophytes of the Driftless Area. A key and annotated list are provided for 73 species, 13 hybrids, and 6 varieties or forms of clubmosses, spikemosses, quillworts, horsetails, and ferns. Included are synonyms, English names, habitat notes, citations of specimens, and comments on Driftless Area populations. The taxonomy reflects the research of the past three decades and is thoroughly modern. The family classification is good, although the *Thelypteris* group is treated as a family separate from Aspleniaceae in spite of their numerous similitaries. A pertinent bibliography is included.

The county distribution maps (based upon collections in 37 herbaria) show not only the ranges within the Driftless Area itself, but also in adjacent parts of Minnesota, Wisconsin, Iowa, and Illinois. Missouri is also included. 54% of the taxa are at the periphery of their ranges in the Driftless Area, and 20% are disjunct. Peck cites several factors to account for these patterns, prominent among which is the absence of glaciation for at least the past 1.5 million years. Of the 13 disjuncts are lobed spleenwort, *Asplenosorus pinnatifidus* (mistakenly called *A. rhizophyllus* on pp. 11 and 108) from the south and the goblin grapefern, *Botrychium mormo*, from the north. The most remarkable disjunct is the Massachusetts fern, *Thelypteris simulata*, the nearest localities for which are in West Virginia and Pennsylvania.

The typography is good, although a few errors have crept in (e.g., *Dryopteris* × *bootii* should read *D*. × *boottii*. Maps 43 and 44 for *Cheilanthes feei* and *Cryptogramma stelleri* have been switched. The scholarship is of high quality. The book should be valuable to all students of the floristics of this part of North America.—W. H. Wagner, Jr.

THE ANNUAL GROWTH CYCLE OF HETERANTHERA DUBIA IN OHIO

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Heteranthera dubia (Jacq.) MacM. (Pontederiaceae) is an aquatic vascular plant indigenous to southern Canada, most of the continental United States, and northern Mexico. In Ohio the plants are most common in the shallow waters of Lake Erie and other lakes and certain streams. The species can be distinguished from other linear-leaved macrophytes by the lack of a petiole and distinct midrib. Because the annual growth cycle has not been completely understood, a detailed study was undertaken.

Populations were observed between May 1979 and September 1980 at three Ohio localities: Put-in-Bay Harbor, Lake Erie, Ottawa Co.; Portage River (a tributary to Lake Erie), 2.4 km west of Elmore, Ottawa Co.; and Big Darby Creek at Amity, 4.8 km south of Plain City, Madison Co. The two Ottawa Co. sites were chosen to show differences between lacustrine and riverine habitats; the third site was selected to observe overwintering. Put-in-Bay Harbor, on the north side of South Bass Island, is connected to Lake Erie, but protected from wave action by Gibraltar Island. The substrate is mud, with some gravel and sand. The most common vascular plants (in decreasing order of abundance), are Vallisneria americana, Myriophyllum spicatum, Potamogeton crispus, Heteranthera dubia, and Potamogeton pusillus. At the second study site, Portage River (about 100 m wide) has wooded shorelines and dolomite outcrops protruding at a slight angle from the riverbed. Submersed aquatic plants associated with H. dubia are Myriophyllum spicatum and Potamogeton pectinatus. Big Darby Creek is narrower than Portage River (20 m wide) with a substrate composed of gravel and sand derived from glacial till. The only submersed aquatic vascular plant present is H. dubia, growing in the riffles where plants were appressed to the substrate by the water current.

OVERWINTERING

Studies by Boylen & Sheldon (1976) and Stuckey et al. (1978) have revealed, contrary to previously interpreted life histories, that several aquatic macrophytes may overwinter as entire plants under ice cover. Monthly observation of populations of *Heteranthera dubia* in Big Darby Creek show that this species too may overwinter as entire plants. Stems do not grow during the winter, when water temperatures are below 8°C, and slowly deteriorate as the winter progresses. By April many leaves are lost, and the

¹Paper no. 52, Aquatic Biology Program, Univ. of Alabama.

TABLE 1. Stem "germination" of *Heteranthera dubia* in laboratory aquaria at 20°C during the normal period of winter dormancy and field notes.

	CREEK WATER TEMPERATURE (°C)	TIME TO GERMINATION (AND FIELD NOTES)
13 Oct. 1979	10	buds seen in 3 days
3 Nov.	_	buds seen in 3 days (many leaves broken)
8 Dec.	4	buds seen in 3 days
18 Jan. 1980	4	buds seen in 4 days (many stems shorter)
17 Feb.	0	buds seen in 3 days
16 Mar.	6	buds seen in 3 days (only a few leaves left)
10 Apr.	9	(slight evidence of growth in the field)
27 Apr.	12	(new growth present and leaves up to 2 cm long in the field)

stems are shorter than in October. Spring growth begins in early May, when the water temperature rises above 8°C, with buds developing at nodes of old shoots.

Submersed macrophytes vary in degree of dormancy. Haag (1979) noted that some aquatics, such as *Potamogeton zosteriformis*, are strongly dormant in winter, ceasing growth with the onset of winter and remaining inactive until spring, even if moved to laboratory aquaria at 20°C. In contrast, *Elodea canadensis* and *Myriophyllum exalbescens* resume growth whenever plants were subjected to 20°C laboratory temperatures.

The extent of winter dormancy was determined by monthly collection of stems from Big Darby Creek and placement in laboratory aquaria at 20°C. Water temperatures were recorded in the field (Table 1), and vouchers were deposited at OS and UNA. Stems were able to resume growth within four days at any time during the winter when subjected to 20°C (Table 1).

Strong dormancy has probably evolved in species that live in climates with a definite seasonal pattern, such as the northern United States and Canada (Haag, 1979). This strategy results in low winter mortality and a high probability of population maintenance over time. The adaptive significance of weak dormancy is that the species can become established earlier in the season than other macrophytes. The weak dormancy of the late emerging *Heteranthera dubia* does not follow this adaptive pattern but seems to reflect its widespread distribution and a generally tropical occurrence of the genus (Cook et al., 1974).

Another means of overwintering is by seeds which are 1.2–1.5 mm long and 0.8–0.9 mm wide with 10–16 membranous wings (Alexander, 1937). Mature seeds are released from the fruit and sink to the substrate where they overwinter. On germination in the spring, seedlings develop, as in other aquatic angiosperms (see Kaul, 1978), and may develop into mature flowering plants within one summer.

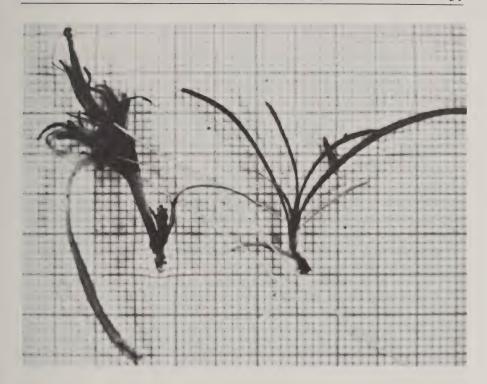


Fig. 1. Overwintering by dormant apices in *Heteranthera dubia*. (Each line represents one millimeter.)

A third means of overwintering is through production of dormant apices (Fig. 1). These structures have leaves that are not greatly modified in shape but smaller than normal (up to 4 cm long and 1–2 mm broad). The stems also have much reduced internodes and may develop roots. Such structures have been previously undescribed for this species. The shorter days and cooler water temperatures of autumn may be the cause of their development. The apex may remain attached to the stem through the winter. Dormant apices appear to germinate in the spring as water temperature increases.

VEGETATIVE GROWTH

Overall plant growth, as observed by Horn (1981) in Put-in-Bay Harbor during 1980, seems to be uniform throughout the summer, yet slower than in many other submersed vascular plants. Harman (1974) also observed in Otsego Lake, New York, that *H. dubia* was slow in developing and remained low in the water column until mid-September when it became the dominant plant, growing above other submersed aquatic plants.

Maximum stem growth was observed to be much greater in Lake Erie than in Portage River or Big Darby Creek. Stems in Put-in-Bay Harbor were as long as 2.2 m, whereas those in the riverine habitats were no more than

1 m long. The greater length is probably due to the greater depth at which the plants are rooted.

Vegetative reproduction is common during the growing season, when stems may break loose and eventually float to a suitable habitat and root.

Stem growth continues into autumn until the water temperature drops below 10°C. Due to the contrasting temperatures at which growth ceases in the autumn and commences in the spring, at least one other environmental factor may be involved, photoperiod. Growth may also be hindered in streams by the development of diatoms on the leaves during late summer.

MUDFLAT PLANTS

The emersed morphology (the mudflat form) develops throughout the growing season as submersed plants become emergent. The leaves of mudflat plants are 25–35 mm long and 1–2 mm broad (submersed leaves being 45–100 mm long and 1–7 mm broad); they are thicker than in submersed plants and have shorter internode lengths.

Mudflat plants have been recognized as Schollera graminea var. minima Coleman (1874), Phrynium dubium var. terrestre Farwell (1924), and Heteranthera dubia f. terrestre Victorin (1929). The taxonomic status has been questioned by several taxonomists, including Steyermark (1963), who considered the form "undoubtedly a mere ecological condition correlated with fluctuating water levels." Observation of herbarium specimens indicates the existence of intermediate forms; hence it was hypothesized that no genetic difference between the mudflat and submersed forms exists. To test this hypothesis, submersed plants were subjected to emersed conditions in laboratory aquaria (see Horn, 1981). When submersed plants became emersed, most of the leaves quickly wilted and died. However, growth at apices and nodes quickly produced leaves with a typical mudflat morphology. Mudflat plants developed submersed-type leaves and longer internodes when placed in an aquarium with 20 cm of water.

In the field, submersed plants may become exposed to emergent conditions by two mechanisms. Loose plants may, by flooding, be partially buried in the gravel and sand of bars and shores during the growing season. Later, as water levels recede, new stems develop out of the water. Also, plants that develop in shallow water of rivers and ponds may become emergent as water levels drop during the summer.

FLOWERING

Inflorescences on submersed river plants become visible in June. Plants in Lake Erie, however, flower later due to the greater depth at which they are rooted. Inflorescence production continues throughout the summer and ceases in September. Flowers are mainly cleistogamous, but chasmogamous flowers may develop on mudflat plants and on submersed plants only when the stems reach the water surface. Cleistogamous flowers are not morphologically reduced (Wylie, 1917; Thieret, 1967; Horn, 1981). Pollination is effected in cleistogamous flowers by the elongation of the stigma past the

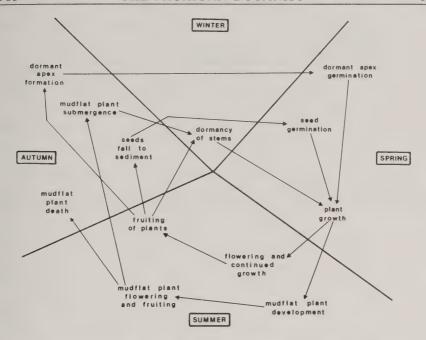


Fig. 2. Annual cycle of growth and reproduction of Heteranthera dubia in Ohio.

mature and open anthers. Seeds develop (mainly from cleistogamous flowers) within three weeks, are released at maturity, and sink to the substrate where they may overwinter.

SUMMARY

Heteranthera dubia has developed a multi-faceted annual cycle (Fig. 2). During the spring and summer it can grow in lakes, ponds, rivers, and streams, both as submersed plants, with stems elongating to the surface, and as mudflat plants. Flowers may be cleistogamous or chasmogamous. The species can overwinter by stems, seeds, and dormant apices.

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NOTICES

Correction. The legend that appears on p. 29 of volume 21 should read (left to right) large sassafras, chestnut oak, and black cherry.

Notice of publication. The third edition of the Mosses of the Great Lakes Forest, by Howard Crum, was published June 21, 1983. Useful throughout the Great Lakes-St. Lawrence River area, this manual includes all the mosses of the state of Michigan. The keys and descriptions have been significantly improved, and all the illustrations have been altered or replaced. The book is available from the Herbarium of the University of Michigan, Ann Arbor, 48109-1057, at a cost of \$15.00 (US) plus postage (\$1.00 in the US, \$1.75 elsewhere).

ASPECTS OF FLORAL BIOLOGY IN THREE SPECIES OF POTAMOGETON (PONDWEEDS), \mathbb{R}^{3}

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Potamogeton is a taxonomically difficult genus of pondweeds containing approximately 90 species that often exhibit considerable vegetative variability. The difficulty is often compounded by hybridization (Fernald 1950; Haynes 1974; Haynes & Williams 1975; Ogden 1943). Investigations of breeding systems could significantly improve the understanding of the genus. Other than observations of pollination, however, relatively little information regarding sexual reproduction is available. The purpose of this paper is to report aspects of the floral biology and pollination of three species.

Many pondweeds are considered anemophilous, *i.e.*, wind-pollinated (Faegri & van der Pijl 1979; Fernald 1950; Haynes 1978; Sculthorpe 1967; Voss 1972). A surface-type pollination mechanism, whereby the pollen floats to the stigma, is also reported (Arber 1920; Proctor & Yeo 1972; Sculthorpe 1967; Yeo 1965). True hydrophily (under-water pollination) is also believed to occur in the group (Haynes 1974, 1978; Proctor & Yeo 1972; Voss 1972), but no experimental evidence has been reported. Entomophily (insect-pollination) is also suggested to occur in the group (Thieret, cited in Haynes 1978).

The breeding systems have not been investigated, although some reports concerning floral biology are available. Faegri & van der Pijl (1979) state that the flowers are dichogamous and thus prevented from self-fertilization. Proctor & Yeo (1972), Muller (1883), and Jaeger (1961) make note of the protogynous nature of the flower.

Field observations and experiments were carried out in New Hampshire in the summer of 1982 on *Potamogeton spirillus* Tuck., in the Contoocook River, Boscawen; *P. epihydrus* var. *ramosus* (Peck) House, in the Bellamy River, Dover; and *P. pusillus* var. *tenuissimus* Mert. & Koch [= *P. berchtoldii* subsp. *tenuissimus* (Mert. & Koch) Cald. & Tayl.], in a small pond near the junction of Mill and Packers Falls Roads, Durham. Inflorescences on 30 plants were bagged with dialysis tubing to determine basic aspects of breeding systems, such as the existence of autogamy. The same number of inflorescences were left unbagged. Fruit production was then monitored.

Potamogeton spirillus

Potamogeton spirillus possesses dimorphic flowers, i.e., aerial and submersed types (Fernald 1932, 1950). Contrary to Fernald, who makes particular note of an apparent lack of anthers in the submersed flowers, I find that

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submersed flowers do possess anthers, although much smaller than those on aerial flowers.

High numbers of fruits produced per plant are considered helpful in identifying *P. spirillus* (Hellquist & Crow 1980). I observe that both aerial and submersed flowers consistently exhibit nearly 100% fruit production. In submersed flowers the anthers appear to dehisce before the flowers open, resulting in self-pollination and fertilization. Due to the small size of the submersed flowers I was not able to determine whether they are dichogamous or homogamous.

In the protogynous aerial flowers the stigmas expand and become receptive before the anthers dehisce, although receptivity lasts until after anther dehiscence. As with the submersed flower the pollen is compatible with the stigma of the same flower. However, self-fertilization can occur only if fertilization has not already taken place during an early period of stigma receptivity. Thus, the aerial flowers of *P. spirillus* appear to be facultatively autogamous. When 30 aerial inflorescences were bagged, all 30 exhibited 100% fruit production, illustrating the autogamous nature.

Potamogeton epihydrus var. ramosus

Potamogeton epihydrus possesses only aerial flowers. Observations on flowering phenology reveal several similarities to the aerial flowers of P. spirillus. The flowers are protogynous. As in P. spirillus, when anther dehiscence occurs the stigmas are still receptive, and self-fertilization results if outcrossing has not occurred. Therefore, P. epihydrus is also facultatively autogamous, with an outcrossing and autogamous phase of flowering. The autogamous nature was illustrated by the 100% fruit production on 30 bagged inflorescences.

Potamogeton pusillus var. tenuissimus

Anthesis takes place on both aerial and submersed inflorescences; however, the flowers are not dimorphic as in P. spirillus. On neither aerial nor submersed inflorescences does fruit production reach anywhere near 100% (mean = 64%, N = 50) as in P. spirillus and P. epihydrus. These observations, combined with the fact that no fruit production occurred on the 30 bagged inflorescences, suggest that the species is an obligate outcrosser.

As the anthers in the submersed flowers dehisce, bubbles form due to the production and release of gas from within the anther sac. The pollen then moves onto the outside of the bubble and is transferred to the stigma. However, this "selfed" pollen does not germinate. Close examination reveals that the pollen often drifts away from the bubble. Thus bubble production may aid outcrossing rather than selfing.

It is apparent that the dichogamous nature of the flowers of *P. spirillus* and *P. epihydrus* is not simply a means of preventing overall self-fertilization. I suggest that the early period of stigma receptivity allows for outcrossing, with autogamy occurring if outcrossing does not take place. Grant (1971) refers to such a system as "predominantly autogamous." *Potamogeton spirillus* seems to have an added character involved in its breeding system. Along with the facultatively autogamous system in aerial flowers there is an obligately autogamous system in submersed flowers.

Through such a facultatively autogamous breeding system a species could, at least occasionally, produce "outcrossed" seeds, thus providing genetic variability in a small percentage of progeny. This variability is believed to be adaptive in a changing environment (Williams 1975). Such a facultative system could also allow for high seed set, assuring the continuation of the population in its present habitat. Seed production is especially important for such annual species as *P. spirillus*.

The relatively large amounts of pollen produced per anther seem to correlate with such a two-phased breeding system, in which one phase (i.e., anemophily) is very unpredictable. A facultatively autogamous breeding system may also help to explain why herbarium specimens often exhibit few nearly mature fruits on a flowering spike, while the majority of fruits on that spike are at an earlier stage of development. Those fruits further along in their development would have been initiated earlier, during the early period of stigma receptivity, and the majority of fruits are further behind in development due to initiation later via autogamy.

Many species of *Potamogeton* are very efficient in their fruit production capacities. If anemophily is, in fact, the primary means of outcrossing, one must doubt the efficiency of such a mechanism given the proximity of the flowers to the water. I believe that a facultatively autogamous breeding system would explain the high numbers of fruits produced. Thus, although anemophily may be the primary outcrossing mechanism, thereby increasing the evolutionary potential, the autogamous aspect of the flower is also an important part of reproduction.

Some species of *Potamogeton* that produce submersed flowers are believed to employ air bubbles to aid in pollination (Wesenberg-Lund 1908). Although these bubbles are reported, the actual mechanism of pollen transfer is not understood. Richardson (1976) reports that some plants of *Ruppia maritima*, a relative of *Potamogeton*, are autogamous, achieving underwater pollination via air bubbles. He notes that "a gas bubble develops from within the anther sac as the anther dehisces, carrying pollen grains out of the theca into proximity with the receptive stigma." Bubble formation in *P. pusillus* seems similar in these regards, although the species appears to be an obligate outcrosser. Here, although self-pollination may take place, the pollen is incompatible with the stigma of the same flower (and probably same inflorescence). Thus, seeds would only be produced via outcrossing.

Because *P. pusillus* produces fruit on both aerial and submersed flowers, some questions arise regarding the different adaptations of the stigma in the two conditions. Ducker & Knox (1976) report that stigmas of aerially pollinated flowers differ from those that are pollinated while submersed. Whether the present case indicates a unique adaptation to both the aerial and submersed conditions or some other specialized pollination system clearly requires further study.

An understanding of breeding systems may offer some explanation for the rare occurrence of fruit production on some pondweeds. For example, *P. robbinsii* seldom flowers and even more rarely produces fruit (Fernald 1950; Hellquist & Crow 1980; St. John 1916; Voss 1972). The common occurrence of the species, often in large populations, suggests that vegetative propagation is the primary means of reproduction. An obligate outcrossing breeding

system could be directly responsible for the lack of fruit production. Even though flowering populations appear to be composed of numerous individuals, these may only represent a single clone. Thus cross-pollination within the clone could not occur due to self incompatibility. Fruit production would take place only when two or more genetically different plants flower simultaneously. However, detailed study of floral biology and breeding systems are required before this aspect of the plants' biology can be understood.

SUMMARY

Investigations on floral biology indicate facultative autogamy for *Potamogeton epihydrus* var. *ramosus* and the aerial flowers of *P. spirillus*; the submersed flowers of *P. spirillus* appear to be obligately autogamous. An obligate outcrossing system is indicated for *P. pusillus* var. *tenuissimus*, which produces a single flower type, although anthesis takes place in both aerial and submersed conditions. In the later case bubbles produced in the anther sac may help disperse the pollen.

I would like to thank Paula K. Busse, and Drs. Garrett E. Crow, Antoinette P. Hartgerink, C. Barre Hellquist, Thomas D. Lee, and Eugene C. Ogden for helpful comments on the manuscript.

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EURASIAN INTRODUCTIONS TO THE MICHIGAN FLORA. I.

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Since the exact time and place of introduction, whether by accident or intention, of many "alien" plants is rarely known, their documentation often lags far behind their appearance in the flora. Identification is often complicated by such regional manuals as Fernald (1950) and Gleason & Cronquist (1963) that, as Shinners (1965) noted, have either ignored aliens or treated them so superficially "that accurate information about them cannot be obtained." If one considers that many such plants have become major "weeds," the documentation process becomes a type of early warning system.

After retracing much effort in identifying an alien plant for the second time, Rollins (1982) was convinced that "all alien plants growing without cultivation should be recorded and made known in some way." With this goal in mind, we present information on six introduced plants: one a "return" invader, four new to Michigan, and one long known to occur here but requiring clarification of status.

Dianthus carthusianorum L.

Figs. 1 & 2

The widespread cultivation of many *Dianthus* species as ornamentals certainly plays a role in their establishment in North America, including quite possibly our new record for Michigan, *D. carthusianorum*, the Cluster-head Pink.

D. carthusianorum is a member of Dianthus subsection Carthusianoides, a group of taxonomically difficult species native to central Europe, the Mediteranean region, and adjacent southwest Asia (Meusel & Muhlberg in Rechinger, 1979). Many problems in the group revolve around D. carthusianorum itself. In his monograph of Dianthus, Williams (1893) listed 35 varieties of D. carthusianorum, noting "as in the case of all polymorphic species with a wide distribution, there is a considerable divergence of opinion as to the definite circumscription of individual forms in the varying degrees of subspecific types." Tutin (in Tutin et al., 1964) favored an opposing view by ignoring infraspecific taxa, noting that variation in a number of characters "seems to be largely continuous and with little

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Fig. 1 (above). Dianthus carthusianorum at Hancock, Michigan, 11 July 1982. Fig. 2 (below). Inflorescence of D. carthusianorum.

correlation between the different characters." We have chosen to accept Tutin's assessment and have not attempted to apply an infraspecific designation to the Michigan population.

D. carthusianorum plants collected near Hancock (Houghton Co.), Michigan, can be distinguished from all other Dianthus species naturalized in the United States by a leaf sheath at least three times as long as the diameter of the stem. Of the naturalized species, D. armeria L. (Deptford Pink) and D. barbatus L. (Sweet William) are most likely to be confused with D.

TABLE 1. Three *Dianthus* species contrasted. Information based on specimens collected in Michigan.

	D. carthusianorum	D. armeria	D. barbatus
Habit	perennial	annual or biennial	perennial
Stem pubescence	glabrous	strigose, esp. below nodes	glabrous
Leaf shape	linear	cauline—linear basal—narrowly oblanceolate	lanceolate
Leaf sheath length	14–18(25) mm	1–4 mm	3–6 mm
Inflorescence	dense capitate head of many flowers	few flowers in terminal open cymes	dense capitate head of many flowers
"Epicalyx bracts"			
color	brown	green	green with ± purplish tint
texture	membranous	herbaceous	herbaceous
shape	broadly ovate, abruptly aristate	linear	ovate, aristate
Calyx	• •		
color	strongly reddened	mostly green	mostly green
pubescence	lobes puberulent	long-villous	glabrous
Corolla color	dark crimson	pink to red with white spots	red spotted with white; pink; wh

carthusianorum (Table 1). Other characters must be used to separate D. carthusianorum from more closely related species. The absence of a modern monograph of Dianthus complicates this process, since no single floristic work includes all of its relatives. Dianthus treatments in four major floras were consulted on the basis of geographic coverage: Flora of Turkey (Reeve in Davis, 1967), Flora of the USSR (Schischkin in Komarov & Schischkin, 1936), Illustrierte Flora von Mitteleuropa (Meusel & Muhlberg in Rechinger, 1979), and Flora Europaea (Tutin in Tutin et al., 1964). In each case, the Hancock material keved out to D. carthusianorum on the basis of the following characteristics: plant not glaucous; leaves linear; uppermost leaves not dilated at base (sheath not inflated); leaf sheath at least three times as long as the stem diameter; epicalyx bracts all brown, distinctly awned, and about one-half (or more) the length of the calvx; calvx less than 15 mm in length with the teeth acute. The presence of pubescence on the calvx and awns on the epicalyx bracts (with the awns sometimes longer than the wide part of the bract) complicates the diagnosis in Tutin, but a careful reading of species descriptions shows that D. carthusianorum is clearly the most likely taxon.

The keys to commonly cultivated taxa provided in Bailey (1949) are often useful since taxa may be included that are not present in any available regional manual. In this case, *D. carthusianorum* is listed, but Bailey's reliance on involucral bract length to distinguish *D. carthusianorum* from the closely-related *D. cruentus* Griseb. is problematic since the character is very variable in *D. carthusianorum*; bract length of Hancock plants clearly ex-

ceeds the range that Bailey states for *D. carthusianorum*. An inspection of the *Dianthus* collection at the Bailey Hortorium (including specimens that Bailey would have consulted in preparing his manual) revealed that he would also consider the Hancock plants *D. carthusianorum*. Eight specimens, six in a folder labeled in his hand "*D. carthusianorum* var. *atrorubens* (*cruentus*, Hort.)" and two others bearing *D. carthusianorum* determinations in his hand, exhibited large, heavily-bracted, long-awned inflorescences, matching the Hancock specimens very closely.

Several common names have been applied to *D. carthusianorum*: Carthusian Pink (Polunin, 1969), Cluster-head Pink (Bailey *et al.*, 1976), Sweet John 'or simply Johns' (Brotherston, 1904), and Wild Pink (Meusel & Muhlberg *in* Rechinger, 1979).

Meusel & Muhlberg illustrated the native distribution as including nearly all of central Europe, with additional stations in southwest Europe, the Balkans, western Russia, and northeastern Turkey. Specimens examined from the United States are listed below. Symbols for herbaria (throughout this paper) follow Holmgren *et al.* (1981).

MICHIGAN. HOUGHTON CO.: Sandy area 15 m W of M-203, 1.7 mi W of M-203–US-41 jct, Hancock, T55N, R34W, S28, NE/4, *Rabeler 659*, 9 Sept. 1981 (BH, GH, MICH, MSC, NY, US); along driveway to former Colonial Steak House (opposite *659*), 1.7 mi W of M-203—US-41 jct, Hancock, *Rabeler 710*, 11 July 1982 (BH, DAO, GH, MICH, MIN, MSC, NA, NY, US).

NEW HAMPSHIRE. COOS CO.: S. slope, Emerton place, in grass, *Deane*, 1 July 1920 (BH); grassland, Prof. E. Emerton's place, Shelburne, *Deane*, 28 June 1926 (PAC).

The Deane collections, labeled *D. atrorubens*, are clearly referable to *D. carthusianorum sensu lato*. Prior to discovering these specimens, it appeared that our Michigan collections represented the first collection of naturalized *D. carthusianorum* in the United States since none of the major manuals for the New England states (Fernald, 1950; Maguire *in* Gleason, 1952; Gleason & Cronquist, 1963; Seymour, 1982) mentioned *D. atrorubens*. Pease, in *A Flora of Northern New Hampshire* (1964), listed *D. atrorubens* as a "Rare escape. *-Shelburne* Deane (14,20,26)," indicating that Deane also collected it at Shelburne in 1914. The statement by Deane on the specimen at BH, "Introd. cult. no where in neighborhood," suggests that he also thought it had escaped.

D. carthusianorum at Hancock occupies an open area of mixed sandy till on both sides of M-203 and, as shown by abundance (several hundred plants), stature (up to 95 cm tall), and abundant seed production, is well established and thriving. Most associated species are common to weedy fields and roadsides—Chrysanthemum leucanthemum (Leucanthemum vulgare Lam., per Rice et al., 1982; Ox-eye Daisy), Melilotus alba (White Sweet Clover), Achillea millefolium (Yarrow), Agrostis gigantea (Redtop), Poa compressa (Canada Bluegrass), and Pteridium aquilinum (Bracken Fern; W. of M-203 only). This population was first noted by Gereau in 1976; D. carthusianorum has thus been in place here for at least seven seasons. The

TABLE 2. Three subspecies of *Medicago sativa* contrasted. Data from Davis (*in* Davis, 1970), Gunn *et al.* (1978), Lesins & Gillies (1972), Lesins & Lesins (1979).

Character	subsp. sativa	subsp. × varia	subsp. falcata
Petal color	violet or lavender, rarely pink or white; monochrome	violet, mauve, greenish, yellow, cream, or white; monochrome or variegated.	yellow or yellow- orange; mono- chrome
Petal pigments	anthocyanins	anthocyanins, carotenoids, flavonoids	carotenoids, flavonoids
Shape of standard (banner) petal	elongate, sides parallel at mid-section	oval, sides not parallel	ovate or obovate, sides not parallel
Pod shape	tightly coiled (1.5–5 coils), with only a small opening in center	loosely coiled (0.5–2 coils), with a large opening in center	straight to sickle- shaped; curvature not exceeding a semicircle (0.5 coil)

source of introduction is unknown, but escape from cultivation some time in the past is likely since Dianthus plants (not D. carthusianorum) were seen in cultivation on the north side of the field containing D. carthusianorum. The size and vigor of this population suggest that D. carthusianorum should be added to the flora of Michigan.

Medicago sativa L. subsp. × varia (T. Martyn) Arcang. (pro subsp.)

Alfalfa is the most important forage crop in the world, with over 30 million hectares under active cultivation in 1972 (Lesins & Lesins, 1979). Much of this land is seeded with hybrid strains derived primarily from two taxa, *Medicago sativa* L. and *M. falcata* L., that, as Lesins & Gillies (1972) noted, "interbreed freely and the offspring have unimpaired viability." Although "pure" *M. sativa* and *M. falcata* can be separated easily on flower and legume characteristics (Table 2), the hybrid progeny can exhibit almost any intermediate combination of characters. The desire to catalog this variation has lead to a proliferation of names in the literature; Lesins & Gillies (1972) stated that "there are over 50 described species and close to 100 names at below species rank" in the *M. sativa—M. falcata—M. glutinosa* M. Bieb. complex. Davis (*in* Davis, 1970), Lesins & Gillies (1972), and Lesins & Lesins (1979) all maintained the above taxa as species primarily on morphological distinctions, with any hybrids considered at the species level. Tutin (*in* Tutin *et al.*, 1968) and Gunn *et al.* (1978) cited the ease of interbreeding, high fertility of resulting progeny, and distinctive though intergrading morphologies as reasons to consider *M. falcata* and several other taxa as subspecies of *M. sativa*. From our investigation of an area near Dollar Bay (Houghton Co.) containing an assemblage of "intermediate" *Medicago* plants, we favor the latter approach and propose the substitution of a hybrid subspecies for previous references to *M. falcata* in Michigan.

Most American floras include entries for both subspecies sativa and falcata (treated as distinct species) but no mention of hybrid taxa. Subsp. sativa has escaped from cultivation on numerous occasions since its initial introduction in Georgia in 1736 (Schery, 1972). Rice et al. (1982) recorded it for every region of the United States and Canada. Subsp. falcata is less widespread. Rice et al. (1982) showed records from the northern United States and adjacent Canada, while Fernald (1950) listed the distribution as "Mass. to Man., s. to Del. and Mich." Swink & Wilhelm's consideration of Medicago in the Chicago region (1979) is an exception to this pattern. They recognized M. sativa and a "pale yellow, or cream-colored, alfalfa... derived from crossing M. sativa with M. falcata," but not M. falcata.

The most conspicuous feature of the plants at Dollar Bay is variation in corolla color; plants had light blue-violet, blue-green, yellow, and creamwhite corollas. If the key in Fernald (1950) is used to identify these plants, flowers more than 5 mm long and the perennial habit separate all of these collections from five of the seven listed species. The next couplet is:

Corolla blue-violet or purple*; legume spiraled through 2 or 3 revolutions.

1. M. sativa 2. M. falcata

Corolla yellow; legume falcate (sickle-shaped) to nearly straight

lands squarely between the two leads.

Lucerne by Schery (1972).

Inspection of each plant reveals a common legume character: the legume is coiled loosely, usually in one \pm complete circle with a large opening in the center, and is covered with appressed, non-glandular hairs. This complicates an otherwise clear choice; a plant with both coiled fruit and yellow corolla

Lesins & Gillies (1972) considered any populations of *Medicago* "sativa" to be of hybrid origin if variation was present in any of the characters (Table 2) that define the pure taxa; this is clearly the case with the Dollar Bay plants. We have determined that these collections (and others noted below) are best referred to one of the most common hybrid taxa, M. sativa subsp. $\times varia [M. \times varia T. Martyn (pro sp.)]$, given the common name of Sand

In keys that recognize hybrids, the Dollar Bay plants are readily separated from both subspecies *sativa* and *falcata*, with the couplet lead to M. $\times varia$ in Davis (in Davis, 1970) adequately summarizing the situation:

Flowers yellow, greenish, cream, white, mauve [moderate purple], or violet; fruit usually curved into $\frac{1}{2}-\frac{1}{2}$ [- (2) in species text] coils, densely adpressed-pilose and with inconspicuous reticulate nerves

5. × varia

The presence of yellow-flowered plants that are not subsp. *falcata* raises an intriguing question: are Michigan records of subsp. *falcata* indeed subsp.

^{*}Although not mentioned in his key, a plant with a white corolla would be referred to *M. sativa* forma *alba* Benke according to *M. sativa* text.

falcata? After inspecting collections labeled M. falcata at MICH, MCTF, MSC, and WMU, we believe that material clearly referable to subsp. falcata has not been collected in Michigan. Each specimen can be determined as subsp. × varia on the basis of corolla color (presence of some bluish pigment, often at the tips of unopened buds) and /or loosely-coiled pods, both features characteristic of the hybrid condition (Table 2).

The only taxon available in North American manuals for white-flowered Medicago plants is M. sativa forma alba Benke. In his description, Benke (1935) noted that the plants differ from typical subsp. sativa only in corolla color. He continued, saying "they key down to M. varia Martyn f. pallida (Alef.) Rouy," but discarded this conclusion since "most varieties or forms of M. varia have mule corollas of changeable or mixed colors during anthesis, not applicable to my specimens." Based on our observations and the inclusion of monochrome corollas by Davis (in Davis, 1970) and Gunn et al. (1978) within subsp. $\times varia$, white-flowered material in Michigan should be carefully examined with both subspecies in mind.

We have determined the following collections as subsp. $\times varia$. (Corolla colors are those at the time of collection; all Rabeler specimens at MSC have both flowers and fruit.)

MICHIGAN. CHIPPEWA CO.: Corolla light yellow, single plant in roadside gravel of M-28, 1.9 mi SW of Hulbert Corners, T45N, R7W, S4, SE1/4, Rabeler 695, 9 July 1982 (GH, MICH, MSC, SMU, US); flowers cream-colored, shoulder of highway M-28 ca. 1.8 mi SW of Hulbert Corners, Voss 15481, 1 July 1982 (MICH, MSC). DELTA CO.: Flowers yellow, road shoulder, T39N, R19W, S34, SE1/4, Henson 1247, 7 July 1981 (MICH). EMMET CO.: Flowers light yellow, local in gravel pit, SE1/4 sec. 35, ca. 5 mi W of Pellston, Voss 14957, 9 July 1977 (MICH, MSC). HOUGHTON CO.: Corolla lemon yellow, Rabeler 704 (BH, DAO, ISC, MICH, MSC); corolla light blue-violet, 705 (DAO, ISC, MICH, MSC, SMU); corolla cream white, 706 (DAO, GH, ISC, MICH, MSC, US); corolla variable (cream to blue-green to light blue-violet), 707 (BH, DAO, ISC, MICH, MSC); all in sandy, cobbly roadside fill, just W of bridge over mouth of Gooseneck Creek, SE of Dollar Bay, T55N, R33W, S33, SE1/4, 11 July 1982. INGHAM CO.: Corolla lemon yellow, single plant in lawn S of Eppley Center, Michigan State University campus, T4N, R1W, S19, NW1/4, Rabeler 726, 22 Aug. 1982 (MSC, NA); corolla light blue, weedy area S of Chessie System tracks, 155 m W of Harrison Rd., E. Lansing, T4N, R2W, S24, SW1/4, Rabeler 727, 18 Sept. 1982 (BH, MSC, NA, TEX); corolla variegated with petals yellow at base, blue-violet at tip, edge of unmown field, E of MSU Laundry, MSU campus, T4N, R1W, S19, SW1/4, Rabeler 728, 18 Sept. 1982 (MICH, MSC, TEX). JACKSON CO.: Flowers yellow, field, gravelly soil, NE1/4 sec. 23, Leoni Twp., C. & B. Horne 135, 25 July 1967 (MICH). KALAMAZOO CO.: G.T.R.R. right-of-way, 1½ mi W of Schoolcraft, C. R. & F. Hanes 1746, 12 July 1936 (WMU); Grand Trunk Ry, Prairie Ronde Twp., C. R. Hanes s.n., July & Oct. 1936 (MICH). SCHOOLCRAFT CO.: Flowers yellow, edge of Beckman Road, T42N, R16W, S27, SE1/4, Henson 1281, 31 July 1981 (MICH).

Lesins & Lesins (1979) noted that the alfalfa usually cultivated in the North Temperate Zone is M. sativa subsp. \times varia, and so it is not surprising that this taxon should appear in Michigan. In his discussion of cultivated forms of M. sativa, Isely (1951) noted that subdivision of M. sativa into taxa such as subsp. \times varia appeared impractical in the United States, suggesting that most variegated alfalfa is dependent on human propagation. He went on

to state that "escaped and ruderal alfalfa populations probably soon blend together." We believe that plants with four (or more?) corolla colors maintained in proximity in one roadside location provide some evidence counter to Isely's statement. Most plants in the area exhibited violet corollas, indicating that subsp. sativa may be present as well. No evidence of intentional cultivation of alfalfa in the immediate area was noted. In discussing hybrid yellow or cream-colored alfalfa, Swink & Wilhelm (1979) noted its presence in seven counties and said that "it will eventually probably be found in all of [the] counties" of the Chicago region. A similar statement may be in order for Michigan.

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On the cover: A tree graveyard, south-facing along Adams Trail, Route 637, Alger County—a reminder of our role as stewards of our natural heritage; photo provided by J. R. Wells, P. W. Thompson, and G. P. Fons

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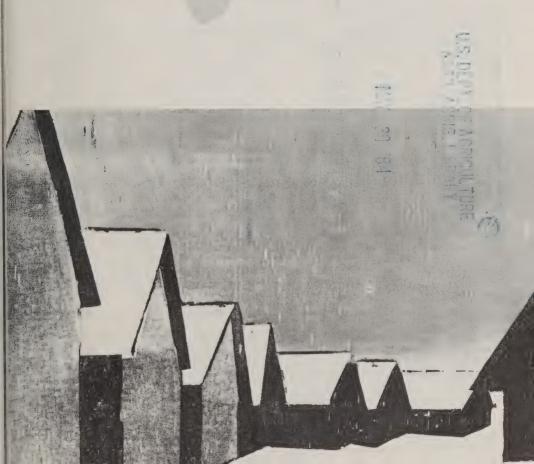
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THE

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March, 1984



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EURASIAN INTRODUCTIONS TO THE MICHIGAN FLORA. II.

Roy E. Gereau

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East Lansing 48824-1312

Richard K. Rabeler

Lyman Briggs School, Michigan State University

Ranunculus ficaria L.

The Lesser Celandine, Ranunculus ficaria, is a favorite old garden plant previously reported as an escape in various localities in the United States and Canada. Rice et al. (1982) listed R. ficaria in their regions 1 (Atlantic northeast coast west to Ohio and Kentucky) and 9 (Pacific Northwest) of the U.S., but not in region 3, which includes Michigan. In Canada, they listed it in regions W and E; Scoggan (1978) listed two occurrences within region E, one in southern Ontario (Wellington Co.). Data provided by Schaffner (1932), Benson (1948), and Gleason (1952) corroborate this distributional pattern, while Keener (1976) added Tennessee (region 2) and Scoggan (1978) added Newfoundland (region M) to the introduced range. No noncultivated North American material from outside the above regions was seen during recent examination of collections at BH, CM, CU, MICH, MSC, MO and PAC. Swink & Wilhelm (1979) reported R. ficaria as spontaneously occurring on the shore of Lake Geneva, Walworth Co., Wisconsin, and along a stream bank at Glencoe, Cook Co., Illinois; these are the only reports known to us from region 3 of Rice et al. (1982).

With spontaneous occurrences as nearby as Wisconsin, Illinois, and Ontario, the lack of reports in Michigan is at least mildly surprising. However, a Michigan collection from the spring of 1982 proved to be of this species:

MICHIGAN. CLINTON CO: 6–7 m from Grand River at mouth of small ravine W of Tallman Rd. (SE of Eagle), T5N, R4W, S34, \$E½, *Gereau 966*, 9 May 1982 (BLH, MICH, MSC, VT).

 $R.\ ficaria$ was found in a small (about 35 \times 30 cm) but well-established patch in an apparently undisturbed woodland. Its associates at this locality, all native species, include $Ranunculus\ hispidus$ (Swamp Buttercup), $Thalictrum\ dasycarpum$ (Tall Meadow Rue), $Phalaris\ arundinacea$ (Reed Canary Grass), and seedlings of $Acer\ negundo$ (Box Elder Maple) and $A.\ saccharum$ (Sugar Maple). Proximity to the river makes origin of seed (or bulbils) from

¹Present address: Missouri Botanical Garden, P.O. Box 299, St. Louis, 63166-0299

an upstream (possibly cultivated) population most likely. In fact, J. F. Keeney (pers. comm.) reported seeing another population of *R. ficaria* in a somewhat similar locality a few miles downstream in the Portland State Game Area (Ionia Co.) in the first week of May 1982. Gereau did not succeed in relocating this population on 9 May 1982, but the site may have been overgrown by other species by that date.

As Keener (1976) noted, *R. ficaria* is unusual among *Ranunculus* species in a number of characters, including number of sepals (3) and petals (7–21). Like much or all of the Canadian material (Scoggan, 1978), our plants are further distinguished by bulbils in leaf axils. In this and other characters (stem height, flower size, petal width), our material fits Tutin's (*in* Tutin *et al.*, 1964) description of the widespread European subsp. *bulbifer* Lawalrée, which has mostly sterile achenes and therefore depends primarily on reproduction by bulbils.

Corynephorus canescens (L.) Beauv.

Gray Hairgrass, Corynephorus canescens, is a perennial European grass of sandy soils, most frequently growing on coastal sand dunes (Hubbard, 1954). Rice et al. (1982) reported this species as introduced in North America in their regions 1, 9, and W. Within the last 50 years, it has been reported from region 1 only on Long Island, New York (Svenson, 1939), and region 9 only at Seattle, Washington (Hitchcock & Cronquist, 1976). While Hitchcock & Cronquist stated that C. canescens is well established in region W on Vancouver Island, Scoggan (1978) made no mention of extant Canadian populations. Earlier reports from region 1 are from Massachusetts (Bicknell, 1914) and New Jersey (Brown, 1879). Wherry (1968) listed C. canescens as a ballast plant in Philadelphia Co., Pennsylvania; although he made no specific comments about this species, he stated that most of the ballast plants were collected between 1855 and 1885, and few had persisted until the date of his publication.

All the above-reported North American occurrences of *C. canescens* are in coastal localities, often associated with ballast-dumping grounds. A recent Michigan collection is therefore the first inland record for North America.

MICHIGAN. BERRIEN CO.: dry, sandy soil at edge of low, grassy, old interdunal depression, T8S, R21W, S17, middle of W½, Reznicek 7124, 16 Oct. 1982 (MICH, MSC).

The remaining two Eurasian species to be discussed are both annuals of weedy habitats. The "ruderal adaptive strategy" (Grime, 1979) of weedy annuals, involving both production of very easily dispersed seeds and a tendency to colonize disturbed and unstable sites, greatly complicates the study of their distributions. Indeed, when the inherent transience of such populations is blended with the usual vagueness of label data on older herbarium specimens, the attempt to locate populations of weedy annuals in the field can become a major exercise in frustration.

Apera spica-venti (L.) Beauv.

Loose Silky-bent (common name *fide* Hubbard, 1954) is a European grass in a small genus most closely related to *Agrostis* (Bentgrasses). The taxonomic characters distinguishing Apera from Agrostis are quite technical and certainly not very easy to observe in the field. However, the only species of Agrostis in Michigan resembling Apera spica-venti enough to cause confusion is the extremely common Agrostis gigantea (Redtop), especially the rather infrequent form with awned lemmas [e.g., KENT CO.: Rogue River State Game Area, Hoffman, Swan & Sarkissian 288, 17 July 1954 (MSC)]. While the majority of the characters distinguishing these two species are microscopic, the presence of rhizomes in Agrostis gigantea and a long-awned

lemma in *Apera spica-venti* serve adequately as field characters.

According to Voss (1972), the only Michigan collections of *Apera spica-venti* were made before 1900: Ingham Co., "near Lansing" (*Bailey* in 1886, GH); and Kent Co., John Ball Park, Grand Rapids (*Fallass* in 1896, ALBC). However, in July of 1980 a specimen submitted for determination at MSC proved to be of this species, and collection the following summer verified its occurrence as an agricultural weed in the "thumb" area:

MICHIGAN. SANILAC CO.: Fertilized wheat field near South Fork Cass River, E. of M-19 between Holbrook and Soule Rds., T14N, R13E. S15, NW1/4, Clayton, 25 June 1981 (CONN, FLAS, ILL, KRAM, LD, LIL, MICH, MIN, MSC, P, UPS, WUD).

With an average height of a little over 12 dm, these plants appear unusually robust as compared to the maximum 8 dm reported in the American literature (Fernald, 1950), and one might be tempted to interpret this as a result of fertilization. However, the technical characters of all the specimens are consistent with the description of the widespread subsp. *spica-venti*, which Tutin (*in* Tutin *et al.*, 1980) reported as reaching a height of 12 dm. McNeill (1981) reported the discovery in 1979 of *A. spica-venti* as a serious weed of winter wheat fields in southern Ontario; proximity in space and time to the Michigan collection suggests that both occurrences may be related to the same recent introduction, probably from Europe. Given the seriousness of the problem in some of the Canadian sites, the abundance of A. spica-venti at the Sanilac Co. site may give cause for agricultural concern.

Chenopodium aristatum L.

Fig. 1

A specimen submitted to MSC by the Cooperative Extension Service, Michigan State University, in the fall of 1981 occasioned considerable difficulty in determination. While quite evidently a member of the Chenopodiaceae and appearing to belong to the genus *Chenopodium* (Goosefoot), the plant differs rather drastically from all *Chenopodium* species commonly reported from the northeastern United States. Instead of the typical arrangement of Chemopodium species are applied to the flowers are ment of flowers in axillary or terminal, congested glomerules, the flowers are solitary in axillary cymes, the lateral branches of which are sterile and terminated by spine-like pedicels. According to *Flora Europaea* (Brenan *in* Tutin *et al.*, 1964), this unusual feature immediately distinguishes the taxon



Fig. 1. Chenopodium aristatum from Alpena, Michigan.

as *C. aristatum*. In fact, Moquin-Tandon (1834) considered this inflorescence type so strikingly different from those of the rest of *Chenopodium* that he transferred *C. aristatum* to its own genus, as *Teloxys aristata* (L.) Moq.; later authors have abandoned this practice.

First described from Siberia (Linneaus, 1753, 1: 221), C. aristatum is a widespread weed ranging from Hungary and the eastern Ukraine through central and northern Asia to Korea and Japan (Iljin in Komarov & Schischkin, 1936; Brenan in Tutin et al., 1964; Ohwi, 1965). Although long reported as occurring in North America, most of the reports of C. aristatum are rather vague and undocumented. Standley (1916) said that it is "reported from Alaska and Mexico' but did not cite any specimens; he admitted in the following year (1917) that its occurrence in Mexico "seems very doubtful." Hultén (1944) considered its occurrence in America "improbable" and later (1968) eliminated it from his treatment of the genus in Alaska. Anderson (1959) and Welsh (1974) similarly failed to mention any Alaskan records of C. aristatum. All reports of C. aristatum in Alaska seem to be based on the report by Ledebour (1851) of specimens from "America rossica" in the Pallas Herbarium, although Ledebour did not claim to have examined this material. Loan requests by Gereau to the curators of B, BM, BR, C, CAS, CGE, FI, G, GJO, H, HAL, LD, LE, LINN, LIV, LZ, M, MANCH, MO, MW, OXF, S, SBT, UPS, and W, the known repositories of Pallas collections (Stafleu, 1967; Holmgren et al., 1981), produced no Alaskan specimens of this species.

After extensive examination of herbarium material, Wahl (1954) could verify only one North American collection: an immature plant from Yonkers, New York (*Bicknell* in 1894, NY). Our 1981–82 investigations of the holdings at BH, CM, MICH, MO, ND, NDG, PAC and WMU revealed no further North American collections, and *C. aristatum* is not listed in either Bassett & Compton (1982) or the *National List of Scientific Plant Names* (Rice *et al.*, 1982). The present collections therefore represent the second verifiable occurrence in North America and certainly the first in Michigan:

MICHIGAN. ALPENA CO.: Lawn at 1333 Golf Course Rd., Alpena, T31N, R8E, S16, NE¼, *Dluzen*, 29 Oct. 1981 (BLH, MICH, MSC, UTC, VT); same locality, *Gereau 1058*, 8 Sept. 1982 (BH, CONN, DAO, FLAS, GH, ILL, ISC, LD, LIL, MICH, MIN, MO, MSC, NA, NY, P, PAC, SMU, TAMU, TEX, UPS, US, WMU, WUD).

The isolated occurrence of *C. aristatum* in Michigan, so far from its previously reported distribution, is certainly puzzling. Aellen (*in* Rechinger, 1979) suggested that the most probable sources of introduction to North America are importation from Asia in grains, oil seeds, or bird food, any of which is plausible enough in the vicinity of a Great Lakes port city. Whatever the method of introduction, *C. aristatum* appears to be thriving in its new habitat. Robert A. Dluzen, the Extension Agicultural Agent for Alpena County, reported (pers. comm.) that *C. aristatum* is widely distributed as a weed of lawns and gardens in Alpena. Its ability to withstand close mowing and a possible (though undocumented) allelopathic effect on other plants give it considerable potential for becoming an economic problem here, as in Siberia (Iljin *in* Komarov & Schischkin, 1936).

We thank the curators of AUB, BH, CM, MICH, MO, ND, PAC, and WMU for hospitality, Joseph Clayton for *Apera spica-venti* specimens and locality data, Robert Dluzen for *Chenopodium aristatum* specimens and locality data, and Janet Keeney and Stuart Ouwinga of the Michigan Natural Features Inventory for discovering the *Ranunculus ficaria* population. The assistance of Kim Chapman, Michigan Natural Features Inventory, in providing literature, and Drs. Edward Voss and Anton Reznicek, University of Michigan, for critical comments on the manuscript is greatly appreciated. The research was supported in part by travel funds to Rabeler from Lyman Briggs School and by funds for preparation of illustrations from the William T. Gillis Memorial Fund.

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REPRODUCTIVE BIOLOGY AND HABITAT OF CIRSIUM PITCHERI,

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Cirsium pitcheri (Torr.) T. & G., Pitcher's Thistle, is endemic to the Great Lakes' shorelines where it occurs on sand beaches and in dune complexes (Fig. 1). It may have originated in the Great Plains area and migrated east to its present range through suitable sandy habitats as the glacier retreated (Moore & Frankton 1963). C. pitcheri is closely related to C. canescens, a characteristic component of the western U.S. Sand Hills flora (Ownby & Hsi 1963).

Cirsium pitcheri is considered rare in Canada (Kershaw & Morton 1976) and Ontario (White et al. 1983). It is currently under review as endangered or threatened in the United States (United States Fish & Wildlife Service 1980). It is on the list of threatened species in Michigan (Wagner et al. 1977), and a permit is required for collection. It is endangered in Wisconsin (Read 1976), threatened in Indiana (Bacone & Hedge 1980), and rare in Illinois (Paulson & Schwegman 1976). Habitat destruction through recreational activity and development is the most significant threat to this species.

In the last decade, *C. pitcheri* was discovered on the north shore of Lake Superior in Pukaskwa National Park. In the park, at its northern limit, *C. pitcheri* occurs on sand beaches which are attractive to park visitors. Since little was known about this rare species, Parks Canada had insufficient data on which to make management decisions concerning this species in the park, and therefore a study was carried out to obtain information on reproductive biology and habitat.

The study was conducted at Oiseau Bay about 25 km south of the Pic River mouth, in Pukaskwa National Park (Fig. 1). Populations occur at Oiseau Bay: (1) at the mouth of Oiseau Creek (817 plants) and (2) on a long crescent beach, 300 m south of the creek mouth (72 plants). These populations are separated by a forested peninsula projecting into Lake Superior. The results reported are based largely on observations of the larger population because sample sizes were very small in the other population. Field work was carried out 10–17 June and 13 July–2 August 1981. Since flowering and seed set were not completed by 2 August, an additional sample of 20 branches from 11 flowering plants was collected on 15 August by park staff. At this time flowering was close to completion and most heads had set seed, but the seed was not yet dispersed.

Plant species and substrate type (sand, litter = thin surface layer of organic matter, debris = thick deposit of organic matter, log) contacting 300 randomly placed cover pins were recorded in each of three habitats. Soil samples 3 cm in diameter were taken to a depth of 10 cm at 25 points, and weight loss on ignition at 400°C was determined.

On 15 July, mesh bags were put over the first or second head of 25 branches on 18 plants before the heads opened. The mesh was sufficiently fine that the stigmas did not protrude. The bags were tied tightly at the base of the heads to prevent insects from entering and to limit



Fig. 1. Distribution of *C. pitcheri* (based on Guire & Voss 1963, White *et al.* 1983 and A. A. Reznicek pers. comm.). Full circles indicate herbarium specimens; half circles represent records from correspondence or literature.

pollen exchange caused by rain and wind. Of the 25 heads bagged, 13 were affected by larvae, and one was removed by a small mammal (judging from the damage). The branches with bags were collected 15 August, and the number of swollen, mature seeds produced in each of the 11 remaining heads was counted. Per cent seed set was determined for each head, and the mean was calculated. Similarly, per cent seed set was determined for 29 first and second heads (on 18 plants) that were not bagged and not affected by larvae. These data were obtained from heads observed in the field and heads in the 15 August sample. Throughout the study, the occurrence of insects visiting *C. pitcheri* heads was recorded, and the relative frequency of occurrence for each species was calculated.

Data on reproduction were based on field observations from 13 July to 2 August, and on the sample of branches collected 15 August by park staff. During sampling, considerable damage to flowering heads from plume moths (*Platyptilia carduidactyla*) was observed. Thus, in addition to describing existing patterns of reproduction, we tried to estimate the impact of plume moths on *C. pitcheri* reproduction. To do this, actual seed set was compared to that which would have occurred in the absence of plume moth damage.

We first had to determine flower production. Since not all heads were observed, we had to estimate missing data. Flower production varied with head size. It was therefore necessary to determine the relationship between head diameter and the number of flowers in a head (assuming no predation). All flowering plants were numbered, and each head was denoted by plant number, branch number, and position on the branch. Head diameter was measured at the widest point on 14 July, and the number of flowers was counted either in the field or in the 15 August sample. A regression equation was fitted (log flower number = 1.42 + 0.037 head diameter in mm; n = 209), and this equation was used to estimate flower production in 61 other heads which still had not opened by 2 August. For heads < 8 mm in diameter, only one flowered as of 2 August and none flowered in the 15 August sample (n = 38). Therefore, estimates of flower production by heads of this size were not considered.

Next, seed production was estimated by determining mean % seed set for 1 mm head diameter classes (8–17 mm) first for 48 heads without larvae, and second for 124 heads with larvae. In classes where no value or only one value occurred, values from the closest diameter class were used in estimation. (This occurred in the 12 mm and \geq 19 mm classes for heads without larvae and in the \geq 18 mm class for heads with larvae.) Seed set for a head was then estimated by multiplying the number of flowers by mean % seed set for the appropriate diameter class; this was necessary for all heads where seed production had not been directly counted.

To estimate seed set for the entire population, in the absence of larvae, values for mean % seed set estimated from heads without larvae were applied to 220 heads (528 heads in total—260 < 8 mm diam.—48 without larvae). To estimate seed set in the presence of larvae, values for mean % seed set with larvae were applied to those heads with larvae, and values for mean % seed set without larvae were applied to the remainder. This estimate included 96 heads for which seed set was estimated (528–260–48–124 with larvae and seed set known).

Seedlings were recognized by the presence of cotyledons. *Cirsium pitcheri* is semelparous; on 11 June and 15 July the area around 54 dead plants was searched. The location of seedlings was recorded within an 8 m diameter circle centred on each plant and divided into four

quadrants.

Confidence intervals, where presented, are 95% confidence intervals on the mean.

RESULTS

In Pukaskwa National Park, the larger population (817 plants—40 flowering, 613 rosettes, 164 seedlings) at the mouth of Oiseau Creek (creek mouth) was separated from the smaller one (72 plants—4 flowering, 41 rosettes, 27 seedlings), on a long crescent beach, by a forested peninsula about 150 m wide projecting 150 m into Lake Superior. Cirsium pitcheri occurred approximately one or two meters above lake level on gently sloping sand beaches in three habitats (in order from lake to land): (1) grass (n = 643 plants), (2) debris (n = 173 plants), and (3) shrubs (n = 1 plant).Table 1 shows that the number of species comprising the vegetation was highest in the debris habitat. Ammophila breviligulata (beach grass) and Equisetum variegatum (horsetail) dominated the grass habitat, Prunus pumila (sand cherry) and Festuca saximontana (Rocky Mountain fescue) were most abundant in the debris habitat, and Juniperus horizontalis (juniper) and Arctostaphylos uva-ursi (bearberry) dominated the shrub habitat. Vegetation cover was highest in the shrub habitat. Substrate types and organic content of the substrate varied among habitats (Table 2) although litter was the most common substrate in all habitats. Organic content was highest in the debris habitat.

Phenology

Seedlings and rosettes were present 10 June when field work began. A few plants that would later flower had very short stalks (< 5 cm) on which a few young heads were visible. By 13 July, all flowering plants had reached their full height. At this time, a few heads (7%) were flowering. The greatest number of flowers were open during the fourth week of July. Seed dispersal began 28 July.

Flowering Plants

Flowering plants ranged in height from 10 to 63 cm (mean = 22 cm), and had from one to 30 branches. Plants at the creek mouth in the grass habitat had more branches (5 \pm 1, n = 31) than plants in the debris habitat (2 \pm 0.3, n = 8) or plants at the crescent beach (1.0 \pm 0, n = 4). The number of heads produced per plant was also higher at the creek mouth in the grass habitat (11 \pm 2, n = 31) than in the debris habitat (5 \pm 2, n = 8) or at the crescent beach (4 \pm 3, n = 4).

TABLE 1. Relative abundance of species in *C. pitcheri* habitat (no. of 300 cover pins touching each species), % cover (% of cover pins touching vegetation), and the number of species of plants touched.

	Grass	Debris	Shrubs
Ammophila breviligulata	62	11	1
Equisetum variegatum	16	5	2
Agropyron trachycaulum	9	12	0
Populus balsamifera	3	0	0
Cirsium pitcheri	2	1	0
Eleagnus commutata	2	5	5
Lathyrus maritimus	2	0	0
Artemesia campestris	2	2	0
Festuca saximontana	1	17	6
Prunus pumila		20	12
Oenothera biennis		6	0
Picea glauca		6	1
Solidago hispida		6	0
Juniperus communis		2	0
Arabis lyrata		1	0
Arctostaphylos uva-ursi		1	20
Juniperus horizontalis		0	53
Anemone multifida		_0	_1_
% cover	28	24	46
Number of species	9	14	9

TABLE 2. The relative abundance of substrate types (%) and soil organic content in C. pitcheri habitats.

	Grass	Debris	Shrubs
Substrate Type			
sand	30	24	32
litter	69	42	68
debris	0	22	(
log	1	12	(
*Organic Content	0.45	1.77	1.25
	± 0.24	± 0.79	± 0.39

^{*%} loss of weight on ignition (means with 95% CI)

Flowering began with the head at the top of the plant. The number of flowers produced in a head is a function of its diameter (Fig. 2), and head size generally decreased from the top to the base. The largest number of flowers per head was 276 and the smallest 30, while the average head (14 mm, mean for creek mouth/grass habitat, n=342) produced 87 flowers.

Pollination

Ten species of insects (2 butterflies, 3 flies and 5 bees) were observed on the flowers (Table 3). Of these, the most frequent was *Bombus vagans*, a bee. All species probed the flowers for nectar secreted by a ridge at the base

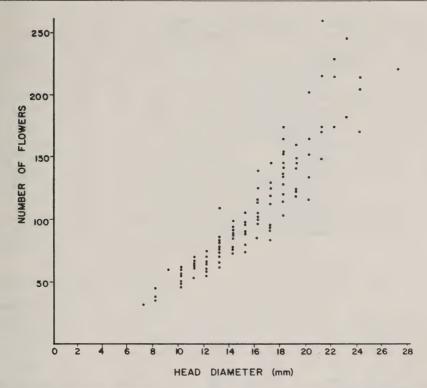


Fig. 2. The relationship between diameter and number of flowers in a head (log flower number = 0.037 head diameter (mm) + 1.42, not all 209 data points shown).

of the style (Knuth 1908). Seed set in heads enclosed in mesh bags to prevent pollen transfer by insects and to limit pollen exchange as a result of wind and rain was significantly smaller than in heads not manipulated (bagged, mean = 4.3%, n = 11; control, mean = 58.2%, n = 29; Mann-Whitney U = 0, p < 0.0001). This suggests that insects may be required for pollination.

Seed Production

Platyptilia carduidactyla (artichoke plume moth) larvae fed on immature seeds and caused flower mortality. In some heads with larvae, flowers did not project beyond the involucre, and in others the flowers opened but died shortly thereafter. Most affected heads had one larva while some had two; the presence of one or more brown involucral bracts typically indicated their presence. When the larva was ready to pupate, it emerged either from the top of the head through the brown flowers or through the side of the involucre. Cocoons were spun in a leaf axil or at the peduncle base. Data for several larvae and pupae collected and reared to obtain adults for identification show that the adults emerge 14 days on average after spinning up. Plume moths were absent from the crescent beach population. For some flowering plants, pupae were found in the rosette centres before stem elongation in

TABLE 3. Insects observed on flowers of C. pitcheri, with frequency (% of n = 36 observations).

Lepidoptera	
Speyeria atlantis	11
Lemenitis arthemis	6
Diptera	
Stratiomys badia	3
Platycheirus inversus	3
Onychogonia yukonensis	8
Hymenoptera	
Bombus vagans	33
B. perplexus	3
Megachile melanophaea	22
M. montivaga	8
Osmia semillema?	3

^{*}total number of observations = 36

TABLE 4. Reproductive output of *C. pitcheri* and the effect of the plume moth.

	Creek	Creek Mouth	
	Grass	Debris**	Crescent Beach
No. flowering plants	31	9	4
Heads/plant—mean	11 ± 2	5 ± 2	4 ± 3
Estimated			
flowers/plant-mean	941	537	456
No. plants with larvae	25	3	0
*Estimated seeds/plant			
without larvae—mean	572	344	289
*Estimated seeds/plant			
with larvae—mean	331	301	289
*Estimated total seeds			
without larvae	17,725	11,412	1,114
*Estimated total seeds			
with larvae	10,196	9,787	1,114
Reduction in seeds due			
to larvae	42%	14%	0%

^{*}without larvae = if no larvae had been present, with larvae = given the observed occurrence of larvae.

June, and larvae were found in the heads in July. Most plants were affected only in July. Table 4 shows that the percentage of flowering plants with larvae was higher in the grass habitat (81%, 25/31) than in the debris habitat (33%, 3/9). Mean seed set estimates were highest for plants at the creek mouth/grass habitat and lowest at the crescent beach. By comparing the seed set values estimated for the absence of larvae to those estimated by taking the effect of larvae into acount (i.e., actual seed set), the effect of the larvae on seed production can be seen (Table 4). In the grass habitat, larvae were responsible for a 42% reduction in seed set compared to 14% in the debris

^{**}for debris, the largest plant (125 heads) was not included in mean calculations since it was atypical. It had 30 branches, whereas the range observed over all other plants was 1–12.

habitat. Large heads might be preferred over small heads as egg-laying sites since the amount of food available would be greater. For C. pitcheri, however, there is no difference in diameter frequency curves for heads with or without larvae [Kolmogorov-Smirnov Test (Siegel 1956) D=0.0303, p>0.10, $n_1=152$, $n_2=190$, creek mouth/grass habitat], indicating that no particular head size(s) was selected for egg-laying. One might also expect the effect of a larva on seed set could be related to head size. If small heads provide sufficient food, then more than sufficient food might be provided in large heads, and therefore some of the seeds in large heads may not be eaten. Figure 3 shows that in all heads less than 14 mm in diameter, no seeds were set (all were damaged). As head size increased beyond this point, the mean number of seeds produced also increased.

In the process of rearing plume moth larvae to obtain adults for identification, one did not develop beyond the pupal stage and an ichneumon parasite emerged from it. Additional work is required to identify the parasite precisely and determine its impact on the plume moth.

Seed Dispersal and Seedlings

The fruits of *C. pitcheri* have a pappus which acts like a parachute for wind dispersal. However, the pappus is delicately attached to the fruit and is easily broken off, hampering long-distance dispersal. The seeds may also remain attached to the receptacle, in which case the head may remain attached to the parent plant or break off as a dispersal unit and be moved by the wind. Dense clusters of up to 42 seedlings were found where seeds attached to a single head had germinated. Figure 4 shows the distribution of seedlings around parent plants. Most individuals occurred downwind (inland) from parents while most clusters occurred upwind (farther toward the lake) from parents.

Seed germination in *C. pitcheri* occurred in June and additional germination was not observed at other times during the summer. Seedling mortality between 11 June and 15 July did not differ between seedlings in clusters (43%) and individual seedlings (28%) ($\chi^2 = 1.92$, p > 0.10, n = 115). Some of the causes of seedling mortality were obvious (e.g. ant undermining in sand adjacent to log—2 individuals) but most were not. Mortality was related to substrate type. For individual seedlings, for example, it was lowest with a debris substrate (12%, 2/17) and highest with a sand substrate (43%, 6/14).

Rosettes

Most of the population occurred as rosettes. Rosette mortality was low; only seven of the 193 rosettes monitored through the study died–(1 trampled by a caribou and 2 by humans, remaining causes not obvious). Plume moth larvae occurred in the centres of some rosettes. Of 99 rosettes in the grass habitat that did not develop flowering shoots, 6% had larvae/pupae only in June, 2% in both months, and 16% only in July. In the debris habitat, examination of 68 rosettes showed that the incidence of larvae was lower (0% June only, 0% both months, 3% July only). The larvae did not appear to cause mortality but damaged the apical meristem.

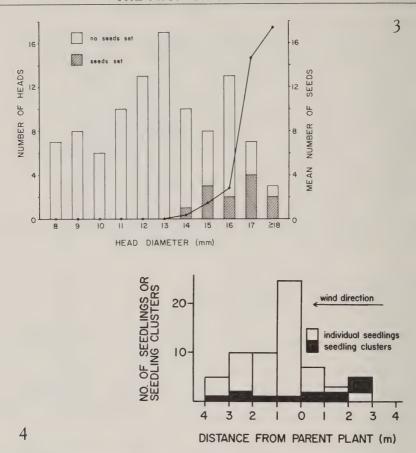


Fig. 3. The relationship between seed set and diameter in heads with plume moth larvae (mean number of seeds). Fig. 4. The distribution of seedlings around parent plants at the creek beach/grass habitat.

Herbivores

In addition to the plume moth, a hymenopteran herbivore was found on $C.\ pitcheri$. Reared larvae did not develop beyond the pupal stage, and adults could not be obtained for identification. This species fed on the leaf surfaces but at a relatively small portion of the leaf (< 10%). The larva spun a short (5 mm) gray cocoon attached to the leaf. This species occurred in less than 2% of the plants at the creek mouth and was absent from the crescent beach.

In addition to insects, two unknown herbivores browsed *C. pitcheri* at the creek mouth. One consumed a portion of the leaves of plants in both habitats (39% plants affected in grass habitat, 35% in debris). In most plants affected, less than 50% of the leaves produced at the time were browsed. As well, it was small, older leaves (not newly developing leaves) that were eaten, and feeding occurred before many leaves had been produced. The other herbivore, a small mammal, browsed the flowering stalks of two plants in the grass habitat but did not consume the heads.

DISCUSSION

C. pitcheri occurs at only two locations on the shoreline of Lake Superior. These isolated populations may have established from seed carried via water currents. Heads have been observed in the water off the Michigan coastline (E. Voss pers. comm.). Alternatively, since open sandy areas would have been much more common near the end of the last ice age, C. pitcheri may have had a more extensive distribution on Lake Superior. Only the Oiseau Bay and Michigan populations may have survived to the present as other sandy areas were covered with dense vegetation. It may be by chance that C. pitcheri exists at these locations rather than at other sandy areas along the shoreline or that C. pitcheri requires very specific habitat conditions which occur only at these two locations.

Cirsium pitcheri is usually referred to as a biennial (Moore & Frankton 1974), implying that a plant grows vegetatively one year, flowers the second year and dies. This, however, is not the case with C. pitcheri or with some other species termed biennial (Werner 1975). Cirsium pitcheri should more accurately be termed a monocarpic or semelparous species—it grows vegetatively for one or more years, flowers once, and then dies (Moore & Frankton 1974). It is likely that flowering is not controlled directly by age but by rosette size reflecting food storage essential for flowering shoot development. This has been observed in other monocarpic species, such as teasel (Werner 1975), and likely applies to C. pitcheri.

The growth form of flowering plants varied between populations and habitats. All plants at the crescent beach were vertical, with one central stalk. Most (89%) of those in the debris habitat at the creek mouth had the same form. In the grass habitat, however, most (84%) were multibranched. These morphological differences are probably related to the occurrence of plume moth larvae in the rosette centres. In rosette centres the larvae feed on the youngest leaves and damage the apical meristem. After several attacks by larvae, year after year, many meristems are produced, each of which eventually develops into a flowering branch, producing a multibranched flowering plant.

When a flower opens, the pistil elongates through the anther tube emerging copiously coated with pollen. This suggests that self-pollination occurred frequently. However, the pollination experiments suggested the importance of insect pollinators in seed production. Mogford (1974) found with *C. palustre* that if cross-pollination did not occur, self-pollination might, but viable seed set was significantly lower. Moore (1975) reported that pollination of *C. arvense* by insects is almost one hundred times more effective in producing seed than wind-pollination. One notable pollinator was an arctic fly (*Onychogonia yukonensis*). Since pockets of arctic plants occur on the north shore of Lake Superior, it is not unreasonable to expect arctic insects as well.

Seed production within a head is influenced both by head size and the plume moth which in turn may be affected by the hymenopteran parasite. The plume moth is widespread from British Columbia east to Quebec and Ontario south to Costa Rica. Larvae have been found on plants in four composite

genera: Cirsium (9 species), Cynara (2 species), Centaurea melitensis (Napa thistle), and Silybum marianum (milk thistle) (Lange 1950). In the large C. pitcheri population, larvae were responsible for reducing seed production by 42% in the grass habitat and 14% in the debris habitat. This difference between habitats may be partially explained by differences in plant density (plants were 1.5 times more dense in the grass habitat). Larvae did not occur in the small population, isolated from the large population by a forested peninsula.

In *C. pitcheri*, seed shadows are formed, and most seedlings occur downwind and close to the parent plants. Dense seedling clusters are found where heads have been buried. Keddy (1982) documented landward movement in fruits of *Cakile edentula* on sand beaches, showing that many were dispersed from areas of good habitat to areas of poor habitat. Dispersal as entire heads rather than separate achenes may thus actually be a method restricting seed dispersal to the narrow band of open beach rather than having all seeds blown inland to shrub and forest vegetation.

Reproductive output and survivorship varied between habitats identified by vegetation, substrate type, and soil organic content. Without experimentation, the causes of this variation remain obscure. Dune plants are known to be limited in growth by nutrient shortages (Pemandasa & Lovell 1974a, Keddy 1981) and by competition from perennial grasses (Pemandasa & Lovell 1974b). Similar experiments could be performed easily with *C. pitcheri*.

Habitat destruction through recreational activity and development is the major threat to survival of this species. In managing it, one must consider not only the plants and their habitat, but also roles of pollinators and the plume moth. In particular, additional information is required on seed germination requirements, the relationship between the plume moth and *C. pitcheri*, and the relationship between the parasite and the plume moth.

SUMMARY

Cirsium pitcheri is a rare endemic on the shores of the Great Lakes where it occurs on sand beaches and in dune complexes. Data on reproductive biology and habitat were collected in the summer of 1981 for two populations located on the north shore of Lake Superior at the species' northern distribution limit. Plants occur in three habitats distinguished by vegetation, substrate type and soil organic content: (1) with grass (Ammophila breviligulata), (2) in accumulated debris, and (3) with shrubs (Prunus pumila, Arctostaphylos uva-ursi). When the study began (10 June), seedlings and rosettes were obvious, and immature flowering stalks were found in a few rosettes. Flowering peaked and seed dispersal began during the fourth week of July. Mean number of heads per plant varied between habitats and ranged from 5 ± 2 to 11 ± 2 . Heads < 8 mm in diameter are unlikely to flower. Ten species of insect visitors (5 bees, 3 flies, 2 butterflies) were observed on C. pitcheri. The artichoke plume moth (Platyptilia carduidactyla) caused a significant reduction in seed set (14-42%) in one population where larvae fed on immature seeds. As well, larvae were found in rosette centres where they damage the apical meristem and ultimately cause multibranched flowering plants. The plume moth was absent from the other population. A hymenopteran parasite was associated with the plume moth. Most seedlings occurred within 1 m of parent plants. The highest mortality (43%) occurred in clusters where seedlings had emerged from entire heads that had been buried. For individual seedlings, mortality was highest with a sand substrate (43%) and lowest with a debris substrate (12%). In managing this rare species, one must consider not only the maintenance of the dune habitat, but also the role of pollinators and such herbivores as the plume moth.

P. T. Dang (Agriculture Canada, Ottawa) identified the plume moth associated with *C. pitcheri*. Pollinators were identified by D. H. Pengelly (U. of Guelph) and H. J. Teskey, J. R. Vockeroth, D. M. Wood, D. H. Kirtsch, and L. LeSage (Agriculture Canada, Ottawa). The cooperation and assistance of the Pukaskwa National Park staff is much appreciated. This work was supported by a contract from Parks Canada.

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A NEW STATION FOR DWARF LAKE IRIS (IRIS LACUSTRIS) IN WISCONSIN,

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A large population of Iris lacustris was discovered recently in Brown County, Wisconsin (Trick, UWGB 04033, 1978). This Great Lakes endemic was previously collected only in Michigan, Ontario, and Milwaukee and Door Counties, Wisconsin (Voss, 1972), and is currently considered a threatened species in Wisconsin. The reported extirpation of the Milwaukee County population (Read, 1976) is supported by recent field work (Alverson, 1981). In Brown County, at the base of the Door Peninsula, Iris lacustris has been found in at least eight contiguous sections of T25N R22E in the Townships of Scott and Green Bay (Alverson, 1981). The Brown County population lies at least 20 miles southwest of the nearest reported Door County location and approximately 100 miles north of the old Milwaukee site. All the segments of this population appear to be associated with the same small drainage system and are closely associated with Thuja occidentalis, the dominant tree species along this drainage. In general, the densest growth of Iris lacustris occurs beneath small openings in the canopy. The most common herbaceous associates are Polygala paucifolia and Pedicularis canadensis. Soils of this area are shallow and underlain by Niagara dolomite.

It is not known whether the population is increasing or decreasing, but the species has successfully invaded several abandoned logging roads, as

well as rights-of-way of active township roads.

Iris lacustris is usually associated with shoreline areas and has previously been reported from only three other significantly inland sites (14, 10, & 2 miles from the shore), all in Michigan (Guire & Voss, 1963). All Brown County plants found to date have been one to two miles inland and 140 or more feet above the current Lake Michigan water level.

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A FIELD SEARCH FOR NEWAYGO COUNTY PRAIRIES BASED ON AIR PHOTOS AND THE SOIL SURVEY

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The dry sand prairies of Newaygo County have held the attention of biologists and conservationists for three decades. These northernmost of Michigan's open prairies have a flora which resembles western dry prairie more closely than other Michigan grassland. Several species rare in the state live here, including Geum triflorum (prairie smoke), Aster sericeus (western silvery aster), Bouteloua curtipendula (side-oats grama), Hesperia ottoë

(plains skipper), and Speyeria idalea (regal fritillary).

Recognizing the phytogeographical and ecological significance of these prairies, the Michigan Natural Features Inventory (MNFI) surveyed the prairie region for relicts of the original grassland. Since hundreds of acres of disturbed secondary grassland exist, even on land which formerly supported forest, the chief criterion was that a stand be unplowed. Secondary considerations were the size of a tract, its quality (diversity, lack of disturbance, etc.), and defensibility as a nature preserve. In this way we hoped to sort through the many adventive and secondary stands to select the finest examples of dry sand prairie for preservation.

The present Newaygo prairies are the result of extensive human disturbance. The history and nature of that disturbance provide clues for finding prairies worth preserving. Southeast Newaygo County once had several large areas of open grassland mingled with smaller openings, oak savanna, oak and pine forests, and a small amount of beech-maple-basswood forest (Hauser 1953) in Brooks, Croton, Big Prairie, and Everett townships. Settlers knew that prairies were fertile (Peters 1970) and planting could begin immediately without clearing the land. Consequently, the open prairie was the first land plowed in the county (Mick 1951). Nearly all was plowed and the irregular edges of the surrounding forest were squared off to form regular fields. The forest was cut (especially white pine) so that there are very few large trees today.

Because the prairie soil was sand, rather than loam as in southern prairies, the soil was easily eroded, especially by wind. Part of Big Prairie eroded so severely that blowouts and dunes formed, earning the name "The Desert" and creating a small tourist attraction (Mick 1951). After a few years of cultivation and relative prosperity (the heyday of farming was between 1850 and 1880), the fertility of the soil dropped (Hauser 1953). Most farms were abandoned before 1900, and these generally became the property of the government and were eventually incorporated into the Manistee National Forest (Mick 1951).

When farmland was abandoned, the prairie plants that had survived at wood edges, in corners of fields, in fence rows, and at roadsides reclaimed

their former domain. Second-growth prairies were common until the U.S. Forest Service (USFS) began planting them to pine in the 1930's, originally for soil stabilization but also to render the barren, open ground eventually productive. Hundreds of acres were planted by the USFS, and today private owners of prairies also plant them with evergreens for the Christmas tree market. From the late 1960's through the mid-1970's off-road vehicles (ORV's) found the level open land of the former prairies to their liking and, through overuse, disturbed or destroyed its vegetation and exposed bare sand in many places. A prairie that had escaped the plow or the pine was disturbed, certainly more than once, by jeeps and dirtbikes.

The only study of the Newaygo prairies was done by R. S. Hauser (1953). He assumed that none had gone unplowed but nevertheless examined the vegetation associated with 32 acres of Sparta loamy sand (fig. 1), the soil which underlaid open sand prairies. The Newaygo prairies, he concluded, were similar to western prairies, particularly the sand and high prairies of Wisconsin, but they had always been weedy and impoverished in characteristic prairie species, a condition magnified by disturbance following settlement. The original surveyor's notes bear him out at least in that the prairies were considered second or third rate, were sparsely vegetated, and sometimes had pine and oak trees or oak brush scattered in them. Hauser found the prairies generally dominated by *Carex pensylvanica* (Pennsylvania sedge), though several of his study plots showed a predominance of grass cover.

Based on Hauser's work, in 1964 the Michigan Natural Areas Council (1979) identified for preservation 440 acres of "dry prairie" on USFS land. All of this was second-growth prairie, and today all is pine plantation. But a direct result of the Council's activities was the establishment, in 1966, of the Newaygo Prairie Ecological Study Area (fig. 1) on 80 acres of USFS land at the south edge of the former Little Scherrar Prairie (Crispin 1980). In 1969, the Michigan Nature Association (MNA) bought land that had been one of Hauser's study areas near the southwest edge of Marengo Prairie (fig. 1), lying north of Little Scherrar and across the Muskegon River (Crispin 1980). The MNA Newaygo Prairie Plant Preserve protected three plants listed as threatened—Geum triflorum, Aster sericeus, and Bouteloua curtipendula—as well as Linum sulcatum (grooved flax), a plant of special concern. The USFS tract protected Geum triflorum as well.

These two preserves encompassed 80 and 110 acres, respectively, though only about 93 acres were actually open prairie before settlement. Consequently, about 1% of Newaygo County's original prairie was preserved, and that not virgin. Since then, however, opportunities for preservation have diminished dramatically as a result of the aggressive afforestation program of the federal government.

Our attempt to find and preserve unplowed, relatively undisturbed prairies required a several-pronged approach. The essential first step was to match 1978 color infrared aerial photographs with the 32 areas of Sparta loamy sand identified by the soil survey (Mokma & Whiteside 1973), pick out the original outline of the prairies, and look for undisturbed portions of them (fig. 2). We eliminated areas that showed plow lines or rectangular patterns, that had circles of *Carex pensylvanica* (which spreads as a circular clone after it colonizes), that were planted into pines, or that had suffered extensive ORV damage. All these details were apparent on the air photos.

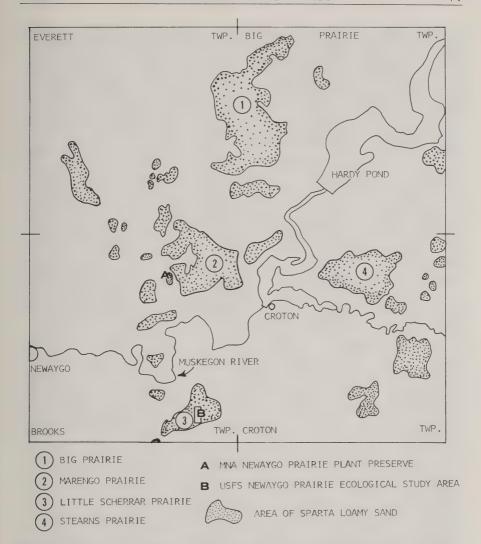


FIG. 1. The Newaygo prairie region showing the location of 32 units of Sparta loamy sand, the four largest historical prairies, and the USFS and MNA preserves (adapted from Hauser, 1953).

Potential unplowed prairies were visited in October 1982. During a preliminary investigation in 1981 we discovered that compared to plowed tracts, unplowed prairie had a high frequency and cover of grass (mostly Andropogon gerardii and A. scoparius), which we took to be a good indicator of naturalness. Indications of past disturbance, usually plowing, were mono-dominant patches of or extensive cover by sedge, high frequency of Rubus flagellaris and the alien weeds Hypericum perforatum and Rumex acetosella, or (of perhaps recent disturbance) indigenous species of sandy areas (Polygonella articulata, Aristida purpurascens, Cladonia spp.).

Besides the vegetation, we considered other factors to evaluate the naturalness of a prairie remnant. Sparta loamy sand has a discrete A horizon, dark-brown because of accumulated organic matter. Below this horizon is a stratum of yellow-brown sand underlaid by pure yellow sand. The thickness of the A horizon told us whether the soil developed under grass or trees or under savanna conditions. Large "savanna trees" on the margins of remnants helped confirmed

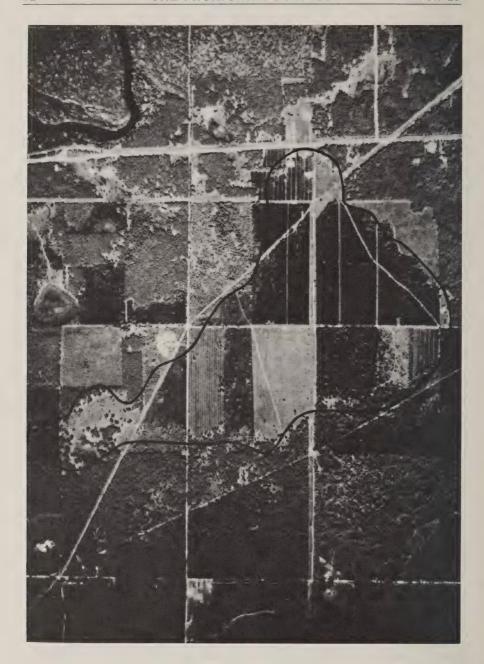


FIG. 2. Aerial view of Little Scherrar Prairie. The unit of Sparta loamy sand (solid line) corresponds to the original prairie, its south edge still plainly visible. The dark areas within the prairie are pine plantations.

that an area was originally prairie because lumbering in the surrounding forest stopped at the edge of the prairies, sparing these trees. Observations on amount of surface soil disturbance, diversity of vegetation, presence of rare plants, and acreage helped us to order the confirmed remnants in a hierarchy that reflected quality as potential nature preserves.

Sparta loamy sand covers 9000 acres of southeast Newaygo County (Mick 1951). The areas of Sparta sand occupy about 9.8% of the fourtownship prairie region and about 1.6% of the county. The four largest areas correspond to Big Prairie (2612 acres), Marengo Prairie (1429 acres), Stearns Prairie (1183 acres), and Little Scherrar Prairie (624 acres). Together these account for 65% of the Sparta loamy sand in the county. The other areas range from 13 to 507 acres, with a median size of 52 acres.

These areas of Sparta loamy sand relate very well to the original extent of former open prairie. At each of the 32 areas, at least one of the following was present: a portion of the original prairie-forest border corresponding to the edge of a unit of Sparta loamy sand; an open, cultivated or formerly cultivated area in an otherwise dense oak woods; or a pine plantation as an island in dense oak woods. Where the original prairie-forest border was intact, the current border lay just within units of Sparta loamy sand, suggesting a slow woody invasion of the prairies.

Of the 17 areas identified from aerials, four we knew about from previous fieldwork. Another four were eliminated by field-checking, leaving 13 unplowed prairie remnants. Eight lay in Brooks Twp., three in Croton, and two in Big Prairie. Including a savanna area, perhaps 66 acres of unplowed grassland were found, about 0.7% of the original open prairie.

The unplowed remnants are all on outwash plain, although six of the original 32 were on pockets of outwash within moraine. One remnant was savanna on Rubicon sand adjacent to an original prairie, and three were mapped as Rubicon adjacent to an area of Sparta, but their soil profile was that of prairie. Soil pH ran from 4.6 to 5 (mostly 4.8). The A horizon was dark brown, or gray in the upper portions, and about 20 to 32 cm thick. Below this was a layer of light brown or yellow-brown sand at a depth of 36 to 46 cm, and under that a thick horizon of yellow sand.

The remnant prairies are set in "bowls" (depressions in the level outwash plain) near historic prairie, lie on the edges of large, historic prairies or isolated, small prairies, or exist in savanna openings adjacent to original prairie (fig. 3). All the prairies but one were bordered by second-growth woods. Large trees grew on the edge of the prairies and within them, while trees of the adjacent forest were generally no larger than 30 cm DBH. Some of the edge trees were quite large: one white pine was 94 cm DBH, and a black oak was 94.3 cm DBH.

Ground vegetation is sparse and low compared to prairies farther south in Michigan. The frequency of grasses is high, and grass cover is good, but *Carex pensylvanica* is one of the three most important species in the virgin prairies. Diversity is poorer than in prairies farther south because only a handful of species are common and the rest rare within any tract. But a large number of species can be found at a site—125 exist in the open bowl of the MNA prairie, for instance. Besides species of dry prairie in Wisconsin and farther west, the Newaygo prairie flora includes several species of open



FIG. 3. An unplowed one-acre opening near the south edge of Little Scherrar Prairie. The large black oak in the left background in 71.5 cm DBH. Oak brush and the forms of the large oaks suggest that the opening was once smaller.

sandy areas, such as dunes (Table 1). This mix of species allies the Newaygo dry sand prairies with barrens.

Six of the prairies supported populations of Geum triflorum, while three had Aster sericeus. Geum triflorum—now restricted in the state to the Newaygo prairies, a small area in adjacent Montcalm County, and Drummond Island— is widespread here, growing in prairies and in the cleared former savanna and woods adjacent to them. Aster sericeus, on the other hand, is limited to areas of former open prairie on Sparta loamy sand. Our discovery of two new populations brings to four the number of extant colonies known in the state and emphasizes the connection of this rare species to its original prairie habitat.

We believe the survey located nearly all virgin prairie of good quality in the region. Possible exceptions include four sites not field-checked because of small size and edge disturbance and three small areas of Sparta loamy sand noted after the survey. The latter are located in Newaygo County, T11N, R14W, Section 28, and Montcalm County, T12N, R10W, Section 6. The sites we visited plus perhaps these additional areas represent the natural grassland of the Newaygo region, all other tracts being second-growth grassland or grassland adventive along roadsides and powerline cuts and in cleared oak woods or savanna. Some smaller units (under 13 acres) of Sparta loamy sand with its associated prairie, missed by the soil survey, may exist as islands within oak forest that was once savanna, but their small size means that they are either nearly overgrown today or are indistinguishable from surrounding open ground which has been cleared of trees.

TABLE 1. Species present in at least three of six unplowed Newaygo sand prairies.

Ambrosia psilostachya (western ragweed) Andropogon gerardii (big bluestem) A. scoparius (little bluestem) Anemone cylindrica (thimbleweed) Arctostaphylos uva-ursi (bearberry) Aristida purpurascens (three-awn grass) Aster azureus (azure aster) A. ericoides (heath aster) A. ptarmicoides (upland white aster) Aureolaria flava (smooth false foxglove) Carex pensylvanica (Pennsylvania sedge) Cladonia spp. (reindeer, etc. lichen) Cyperus filiculmis (nut grass) Danthonia spicata (poverty oat grass) Eragrostis spectabilis (tickle grass) Euphorbia corollata (flowering spurge) Fragaria virginiana (wild strawberry) Geum triflorum (prairie smoke) Gnaphalium obtusifolium (cudweed) Helianthus occidentalis (western sunflower) Hieraceum longipilum (hairy hawkweed)

Koeleria macrantha (June grass) Liatris aspera (rough blazing-star) L. cylindracea (dwarf blazing-star) Opuntia compressa (prickly pear cactus) Panicum depauperatum (panic grass) Panicum commonsianum (panic grass) Panicum oligosanthes (panic grass) Pinus strobus (white pine) Polygala polygama (purple milkwort) Polygonella articulata (jointweed) Potentilla arguta (prairie cinquefoil) Prunus serotina (black cherry) Quercus velutina (black oak) Rosa carolina (pasture rose) Rubus flagellaris (northern dewberry) Salix humilis (prairie willow) Solidago nemoralis (gray goldenrod) S. speciosa (showy goldenrod) Sorghastrum nutans (Indian grass) Tephrosia virginiana (goat's rue) Viola pedata (bird's-foot violet)

The aerial photo work for the survey took about an hour to complete, and field-checking required 18 hours. Our experience is that in searching for virgin plant communities, initial aerial photo work takes relatively little time and saves many hours of subsequent fieldwork. Such surveys not only locate fragments of our aboriginal landscape, but uncover rare species that prefer or require aboriginal habitat. As a result of the survey we determined that the top four stands (two from previous fieldwork) should be protected as nature preserves. The next four deserve voluntary landowner protection. With the goals thus defined, efforts to protect the remaining unplowed tracts of Newaygo dry sand prairie can be coordinated to insure that this unique natural heritage will not be lost.

This study was made possible by a grant from the Living Resources Program, Michigan Dept. of Natural Resources. We thank Dr. D. L. Mokma of the Dept. of Crop and Soil Sciences, Michigan State University, who kindly lent us equipment. Mary Huhn, Michigan Dept. of Natural Resources, Wildlife Division, has our thanks for typing the manuscript.

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NEW COMBINATIONS IN THE GENUS SARCODON.//

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At the International Botanical Congress in Sydney, Aug. 1981, it was voted to conserve *Hydnum* Linnaeus, Sp. Pl., 1178. 1753:E. M. Fries, Syst. Mycol. 1: 397. 1821. Type *H. repandum* Linnaeus:E. M. Fries (typ. cons.). As a result *Hydnum* (Fr.) S. F. Gray, type *H. imbricatum* L.:Fr., becomes invalid and *Sarcodon* Karst., type *Hydnum imbricatum* L.:Fr., valid. Thus, it is necessary to make new combinations for a number of species described by the present author in the genus *Hydnum* as typified by *H. imbricatum*:

Sarcodon piperatus (Coker ex Maas G.) comb. nov.—Hydnellum piperatum Coker ex Maas G., Persoonia 2: 476. 1963. Sarcodon piperatus Coker, J. Elisha Mitchell Sci. Soc. 55: 373. 1939, nom. illeg. Hydnum humidipes K. Harrison, Mich. Bot. 19: 75. 1980.

Sarcodon ustalis (K. Harrison) comb. nov. *Hydnum ustale* K. Harrison, Can. J. Bot. 42: 1215. 1964.

Sarcodon cyanellus (K. Harrison) comb. nov. *Hydnellum cyanellum* K. Harrison, Can. J. Bot. 42: 1214. 1964.—A serious error; the latter should have been published as *Hydnum cyanellum*. Sarcodon subincarnatus (K. Harrison) comb. nov. *Hydnum subincarnatum* K. Harrison, Can. J. Bot. 42: 1216. 1964.

Sarcodon calvatus (K. Harrison) comb. nov. *Hydnum calvatum* K. Harrison, Can. J. Bot. 42: 1216. 1964.

Sarcodon calvatus var. **odoratus** (K. Harrison) comb. nov. *Hydnum calvatum* var. *odoratum* K. Harrison, Can. J. Bot. 42: 1217. 1964.

Sarcodon lanuginosus (K. Harrison) comb. nov. *Hydnum lanuginosum* K. Harrison, Can. Dept. Agr. Publ. 1099: 20. 1969.

Sarcodon rimosus (K. Harrison) comb. nov. *Hydnum rimosum* K. Harrison, Can. J. Bot. 42: 1212. 1964.

Sarcodon subfelleus (K. Harrison) comb. nov. *Hydnum subfelleum* K. Harrison, Can. Dept. Agr. Publ. 1099: 28. 1961.

Maas Geesteranus' transfer of *Hydnellum nigellum* K. Harrison (1974) to *Sarcodon* is rejected. The taxon is typical of *Hydnellum* even to indeterminate growth. The context lacks the hard woody character of many species of *Hydnellum*, but it is scissile and similar to that of the phellodons.

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SEXUAL REPRODUCTIVE CYCLE OF THE LIVERWORT CONOCEPHALUM CONICUM

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The appearance of various life events (birth through reproduction to death), in a liverwort, often called the life history, is generally described in terms of form and structure. Rarely is there any attempt to correlate life changes with the time of year. However, the seasonal and concomitant environmental changes play a significant role in regulating the growth and development of the various stages of the life cycle.

We have observed the complete sexual life cycle of *Conocephalum conicum*, a perennial thalloid liverwort of widespread occurrence in Michigan, and have recorded in succinct tabular format (Table 1), the sequence of events month by month. Although the cycle is continuous, the arbitrary month-by-month records serve as the best pragmatic approach for checking and recording field observations and correlating all the independent events in what turned out to be a 21-month reproductive cycle.

Spring is the great awakening season. All the trees are waking up; the floral stalks of the wild flowers are issuing forth from underground perennial parts, and *Conocephalum conicum* too has its hydraulic lift to raise the fruiting head and shower the spores, while the young male of the species emerges from dormancy and undergoes growth and development in concert with the female. Because of this upsurge in growth and development, we chose March rather than January as an appropriate month in which to break into the continuous life cycle in setting up our tabulation.

Our year round field observations, aided by a pocket lens and aug-

Our year round field observations, aided by a pocket lens and augmented by microtomed sections to confirm the existence of newly initiated sex organs, have brought into sharper focus the following aspects (details in table 1) of the reproductive cycle:

1. Archegonia are initiated in August, fertilized in June of the *following* year; the sporophyte matures in the fall and the spores are shed in spring of the next year—a 21-month cycle spanning three calendar years.

2. The sex organs have attained levels of differentiation analogous in complexity to that of the floral buds of flowering plants when development is

arrested *prior* to their respective overwintering periods.

3. During the ontogeny of the sex organs, remarkable circumlocutions are brought about by differential growth which in terms of form-physiology interrelations may be controlled by even more complex mechanisms than those of the photo-geotropic equilibria phenomena that the liverworts have in common with other plant groups.

TABLE 1. The life cycle of Conocephalum conicum.

	Male	Female	Sporophyte
March	Activation of growth of overwintering shoot.	Breaking of dormancy. Stalk elongation, lifting the head out of the socket and raising it high above the thallus. Development of endosporic gametophytes.	Elevation of sporophytes The sporophytes are passively carried aloft as a function of their attachment to the female head.
		Resumption of growth and differentiation in the embedded archegonio-phore.	
	Lateral expansion of the antheridial disc, enlargement of antheridia, and initiation of pore on the roof of the antheridial cavity.	Completion of stalk elongation. Stalk and head shrivel once the attached sporophyte has released its spores.	Shedding of multicellular spores from capsules on completion of the elevation of the sporophytes.
April	cavity.	Initiation of the lateral displacement of arche- gonia. Archegoniophore remains completely immersed in thallus tissue.	
	Completion of the lateral expansion of the antheridial disc which is attached by a short stalk to the thallus. Maturation of antherozoids (sperm).	Growth and differentia- tion of young game- tophytes. Necrosis of stalks and heads of the remaining stragglers.	Total necrosis of all sporophyte tissues in concert with the stalks and heads, in a few late maturing stragglers.
May		Lateral displacement of archegoniophore completed.	
way		Archegoniophore continues to remain completely immersed in the thallus tissue and a protective outer covering of overlapping ventral scales. Maturation of arche-	
		gonia.	
	Discharge of antheridia and further release of sperms through the pore of the roof of the an- theridial cavity.	Empty sockets (sites of former attachment of stalked heads), visible on thallus.	Total demise of spor- ophyte and sporophyte bearing apparatus re- flected in empty sockets of thallus.
June		Fertilization of archegonia. Archegoniophore covered by overlapping scales	Development of zygote and a few-celled embryo

only.

TABLE 1. (Continued)

	Male	Female	Sporophyte
July	Initial development of two new branches lateral to the empty antheridial disc.	Conical tip of carpo- cephalum slightly pro- truding above the dorsal surface of the thallus, and showing above the new socket.	Differentiation of embry into foot, seta and capsule.
August	Continuing growth of the two lateral branches displaces the empty antheridial disc to an axillary position. New antheridial bud-like shoots are initiated at the tips of the two thalloid branches.	Pronounced protrusion of the top of the coneshaped carpocephalum from a socket in the thallus tissue. Archegonia are initiated at the tips of the thallus branches to each side of the socket of the developing carpocephalum. They are further located on a pad on the floor of a cave-like indentation behind the apical notch and below the zone of air chambers.	Differentiation of spore mother cells and elaters in the capsule of the sporophyte.
Contombou	The empty antheridial discs have attained the characteristic purpleblack coloration.	Initial slight elongation of stalk but the cap is still only semi-emergent from the socket.	Meiosis is complete. Formation of tetrads of non-tetrahedral meio- spores (spores).
September	The spherical bud-like antheridial shoots have a yellowish-green pigmentation.	Archegonial pad bulges upward.	
October	Empty antheridial discs persist. In the bud-like antheridial shoots, the differentiation of antheridia	Cap protrudes prominently above the socket. Upward bulging archegonial pad tips forward. It is still located within	Maturation of unicellular spores and unispiral to trispiral elaters.
	is complete.	the cave but now dis- placed toward the open- ing.	
November	All tissues and sex organs (antheridia) going into dormancy.	All tissues and organs (archegonia) going into dormancy.	Sporophytes going into dormancy.
December January February	All phases of the life and undergo a 3-mon	cycle are blanketed in snow th dormant period.	,

4. The unique non-tetrahedral tetrads first reported by Meyer (1929) and the dimorphous unicellular spores are often overlooked because of the emphasis placed on the multicellular spores or endosporic gametophytes.

These findings point to areas that have not been fully explored in the past and should instill viability in future research. They demonstrate above all else the excitement of year round bryologizing in Michigan for professional and amateur alike.

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REVIEW

THE PRAIRIE PENINSULA—IN THE "SHADOW" OF TRANSEAU: Proceedings of the Sixth North American Prairie Conference. Edited by Ronald L. Stuckey and Karen J. Reese. Ohio Biological Survey Biological Notes No. 15. College of Biological Sciences, The Ohio State University, Columbus, Ohio 43210. 1982 ["1981"]. 278 pp. \$15.00 postpaid.

The Sixth North American Prairie Conference was held August 12–17, 1978, at The Ohio State University, Columbus, so it is not surprising that many of the papers refer to the history, composition, distribution, literature, and other aspects of prairies in Ohio. The concept of the "Prairie Peninsula" is explored. Paul Thompson, Margaret Kohring, Kim Chapman, Robert Pleznac, and Michael Fleckenstein report on Michigan prairies. Material pertaining to other states ranges from Minnesota to Missouri, Texas, and Kentucky. Many historical nuggets are scattered throughout, with special reference to Edgar Nelson Transeau, who received his Ph.D. from The University of Michigan in 1904 and began his distinguished professional career by teaching at Alma College. Other contributors to the development of the Prairie Peninsula concept, each rating a full page with photograph, brief data, and relevant quotation, include several with connections of one sort or another with the state of Michigan: Asa Gray, Henry C. Cowles, C. C. Adams, H. A. Gleason, J. H. Schaffner—and Paul B. Sears, the only living member of that select gallery and who presented a paper at the conference. E. Lucy Braun is the subject of three additional pages of "Memories" by Lucile Durrell—a fascinating sketch of this extraordinary botanist (and her patient sister, Annette), who inspired so many of us. (One day shortly before Christmas, 1953, will forever stand out in my own graduate student career as the day I visited the Braun sisters at their home in Cincinnati, nibbling on popcorn balls and hearing about the glacial border from one who spoke with authority!)

This well produced volume contains all papers submitted by those who presented them at the conference, abstracts for those not submitted, a brief previously unpublished paper by Transeau on "The Vanishing Prairies of Ohio," three selections of "prairie poetry," and even a [mercifully] short comedy skit. There is something in this for eveybody—a much more useful

publication than many conference proceedings.

-E. G. Voss

APPARENT HEAT STIMULATION OF BURIED SEEDS OF GERANIUM BICKNELLII ON JACK PINE SITES IN NORTHERN LOWER MICHIGAN*//

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The germination of buried seeds is an important mechanism of species establishment during secondary plant succession in many ecosystems (Sweeney 1956, Major & Pyott 1966, Ahlgren 1979a, Hall & Swaine 1980, McGraw 1980). The appearance of a large variety of species, not seen on unburned areas, following fire has been attributed to stimulation of germination of buried seed (Went et al. 1952, Sweeney 1956, Floyd 1966, 1976, Christensen & Muller 1975a, Shea et al. 1979). Various factors resulting from fire have been implicated in this phenomenon. Went et al. (1952) reported that removal of competition was a major factor in the abundant germination of chaparral species the first season after fire. McPherson & Muller (1969) concluded that heat from fire degrades some substance in the soil which otherwise suppresses germination of chaparral species. The abundance of the annual Senecio sylvaticus on one-year-old burned Douglasfir (Pseudotsuga menziesii) clearcuts and its disappearance thereafter have been attributed to soil nutrient changes associated with burning (West & Chilcote 1968). Rupture or alteration of the water-impermeable seed coat of hard-seeded species allowing germination has been attributed to fire (Floyd 1966, Cushwa et al. 1968, Martin et al. 1975, Purdie & Slatyer 1976, McDonough 1977).

Germination of many species is restricted to the first year after fire (Horton & Kraebel 1955, Sweeney 1956, West & Chilcote 1968, Purdie & Slatyer 1976). On jack pine sites in northern lower Michigan, Abrams & Dickmann (1982) reported that many species on one-year-old burns were not present on the site the following year. The most striking example was *Geranium bicknellii* Britt., classified as an annual or biennial by Fernald (1950). This species represents as much as 22% of the vegetational cover on first-year burns, but by year two it was not present or was reduced to scattered individuals. It was hypothesized, therefore, that heat from fire was responsible for the appearance of this species on one-year-old burned sites.

In a preliminary experiment with freshly matured geranium seed pretreated with various combinations of moist heat and stratification, no unscarified seeds germinated. In contrast, 80 to 100% of seeds scarified by nicking the radicle-end with a razor blade germinated, regardless of pretreatment (Abrams 1982). These results suggested that if heat was involved in

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geranium germination, a period of dormancy in the soil was required before heat exposure was effective. To test this hypothesis, an experiment was initiated using soil samples collected from different-aged jack pine stands. The objective of this experiment was to determine if heat was involved in the germination of geranium seed buried in the forest floor. It was also possible to compare the germinants from buried seed with the existing flora of each site.

Three different-aged jack pine stands representing a post-fire successional sequence were selected for study: a clearcut area that had been prescribed burned 3 years previously, a 35-year-old post-fire jack pine stand and a 55-year-old jack pine stand of unknown origin. All

stands were located in Ogemaw county in northern lower Michigan.

On May 12, 1981, 12 randomly located soil samples were collected from each site. The samples were 25 × 25 cm in area and 2.5 cm deep into mineral soil. The volume of each sample varied with the depth of the overlying organic material. Samples were bagged separately and air-dried in the laboratory until May 30, 1981. After removing all green vegetation, each sample was sifted through 60 mm mesh screening to remove larger twigs, roots, and rocks. Four treatments (unheated control, heated at 70° for 30 min., heated at 90° for 30 min., and heated at 70°C for 30 min. + stratification) replicated 3 times, were randomly assigned to 1352 cm³ subsamples taken from the screened soil samples from each site. Heated samples were placed in metal trays, moistened slightly, and placed in a forced-air drying oven. To raise samples to and maintain them at 70°C for 30 min., they were first exposed to 150°C for 20 min. (preheating), followed by heating at 100°C for 30 min. The 90°C for 30 min. treatment involved preheating samples at 180°C for 30 min. followed by heating at 120°C for 30 min. During the preheating, samples were periodically stirred and moistened throughout. No additional stirring or moistening was done during the final heating period. A thermometer was inserted into the center of each sample to monitor temperature during heating. In both the 70°C and 90°C heating regimes the samples remained moist through the final heating period.

All samples were next placed over a 3.5 cm layer of sterilized sand (autoclaved at 121° C for 60 min.) in $26 \times 52 \times 6.5$ cm plastic flats. The samples were spread evenly over the sand to form a layer 1 cm deep. The flats designated for stratification were placed in refrigeration (1–2°C) for 8 weeks. All other flats were placed under "cool white" fluorescent lights in a completely randomized design. The flats were exposed to a 14 hour photoperiod with an approximate photonflux density of 35 microEinsteins m⁻²s⁻¹. Temperatures fluctuated between 20 and 25°C. Two flats containing only sterilized sand were used to detect possible contaminants to the experiment. The flats were systematically rotated once a week to reduce possible positional effects. Germination counts were made every two days for the first month and once or twice a week thereafter. After stratification was completed, those flats were placed under the light trays with the other flats. Samples were kept moist throughout the experiment by adding tap water every 1 to 2 days. During stratification, samples were watered every 7 to 10 days. Germinants were recorded as they appeared. Individuals not readily identifiable were removed, potted, and grown until they could be identified. The experiment was concluded after 18 weeks.

At the conclusion of the buried seed experiment, unheated control flats from the 3-year and 35-year-old sites were heated to 70°C for 30 min. using the above procedure to determine if geranium seeds in those flats would germinate when exposed to heat.

No seeds germinated in the flats containing only sterilized sand. However, three seedlings of *Oxalis* sp. came up in other flats and were considered contaminants; this species had not been found on any of the jack pine sites studied in northern lower Michigan.

Most of the germinants appeared during the first 2 weeks of the experiment (Fig. 1). A moderate amount of germination occurred from weeks 3 to 8 and very little thereafter, but there were differences among species (Fig. 2). Geranium germination peaked the first week but had concluded by the fourth week. A substantial number of grass seeds germinated during the second

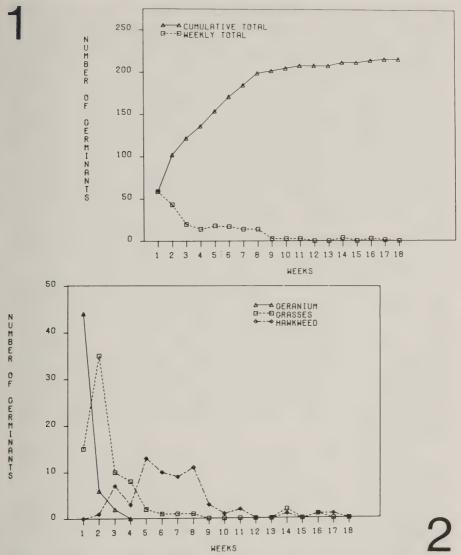


Fig. 1. Cumulative and weekly number of germinants from the control, 70°C—30 min., and 90°C—30 min. treatments in 3-year-old, 35-year-old and 55-year-old sites (combined) during the buried seed experiment. Fig. 2. Weekly total number of germinants of geranium, grasses (all species combined), and hawkweed (*Hieracium* spp.) from control, 70°C—30 min., and 90°C—30 min. treatments in the 3-year-old, 35-year-old and 55-year-old sites (combined) during the buried seed experiment.

week. Peak germination of hawkweed (*Hieracium* spp.) occurred between weeks five and eight.

When heated treatments (70°C, 90°C, and 70°C + stratification) are compared to the unheated controls at each site, striking differences in species composition and number of germinants are evident (Table 1). Most importantly, geranium seedlings appeared only in the heated treatments from

the 3- and 35-year-sites. Differences in the number of geranium germinants in the 90°C and 70°C + stratification treatment compared to the unheated controls were significant (P < .05) using Wilcoxon's nonparametric two sample test (Steel & Torrie 1960). No seeds of geranium germinated in samples from the 55-year site.

Only a few seeds of grasses and sedges germinated in the heated treatments from any site. In contrast, 58 and 22 grass and sedge germinants were recorded in the control flats from the 35-year and 55-year sites, respectively. The differences in the number of grass and sedge germinants between the heated and control treatments from all sites were significant (P < .01) using Wilcoxon's two sample test. Total number of germinants in treatments from each site ranged from 0 to 65, but these differences were not significant. However, the most frequently occurring species in each treatment from the sites differed. For example, 68% of the germinants from the 3-year site were geranium, whereas 71% of germinants on the 35-year site were grasses. Hawkweed, with 36 germinants, was the dominant species on the 55-year site. However, grass species and wintergreen (Gaultheria procumbens) also were important members of the buried seed pool on this site.

Many important members of the plant community observed on the sites did not appear as emergents from buried seed. Noteworthy was the scarcity of seedlings of *Carex* and absence of blueberry (*Vaccinium* spp.), both ubiquitous components of jack pine sites in northern lower Michigan. Also, many species that germinated from buried seed were not surveyed on the respective sites. Examples were wintergreen and *Chimaphila umbellata* (common pipsissewa) from the 3-year site; geranium, *Antennaria neglecta* (field pussytoes), wintergreen, *Panicum capillare*, and common pipsissewa from the 35-year site; and hawkweed, *Viola adunca* (hooked-spur violet), *Danthonia spicata*, *Dichanthelium depauperatum*, and *Panicum capillare* from the 55-year site.

When control flats from the 3-year and 35-year-old sites were heated, one flat from the 3-year site produced 7 geranium germinants and two flats from the 35-year site produced 2 and 3 geranium germinants.

Many chaparral species common to recently burned areas produce seeds which remain dormant in the soil between fires (Sweeney 1956, Christensen & Muller 1975b). Heat treatment has been shown to release seeds of several chaparral species from endogenously enforced dormancy (Stone & Juhren 1951, Sweeney 1956, Christensen & Muller 1975a, 1975b). Consistent with geranium germination in this study, germination of buried seed of certain chaparral species occurs after heating soil samples, whereas freshly matured seed does not germinate after heat treatment (McPherson & Muller 1969, Christensen & Muller 1975a). Christensen & Muller (1975a) speculated that germination of these species may be dependent on the gradual deterioration of seed tissue imposing mechanical restriction of the embryo. Dormancy of seeds stored in the soil for long periods may also result from chemical inhibition by neighboring vegetation. Researchers suggest fire removes the source of toxins (e.g. shrub foliage) and denatures residual chemicals in the soil, thereby allowing increased germination of many species (Muller et al. 1968, McPherson & Muller 1969, Christensen & Muller 1975a, 1975b).

TABLE 1. Total number of germinants for species appearing in soil samples from the 3-year, 35-year-, and 55-year-old post-fire sites during the buried seed experiment. Treatments were an unheated control, 70°C—30 min, 90°C—30 min, and 70°C—30 min + stratification.

		3	3-year			3	35-year			55	55-year	
Species	cont	cont 70°C	2,06	70°C + strat	cont	cont 70°C	2.06	70°C + strat	cont	70°C	2.06 2.0L	70°C + strat
Annual herbs Geranium bicknellii		6	32	23		-	10	4				
Perennial herbs Antennaria neglecta Fragaria virginiana Hieracium spp. 1	-	6	2 -2		2 - 6		_		21	15		-
Woody perennials Chimaphila umbellata Gaultheria procumbens		2		-	-			-	10	8		
Grasses and sedges Carex spp. Danthonia spicata Dichanthelium depauperatum Oryzopsis pungens Panicum capillare		-			28476				2 - 1 -	7 -		
Poa pratensis Unidentified grasses Treatment totals	7 2	21	37	24	17 2 2 65	8	=	S	1 1 56	22	0	-

¹Hieracium aurantiacum and H. venosum

However, abundant germination of many hard-seeded species following fire has been attributed directly to alteration of the seed coat by heat (Cushwa *et al.* 1968, Purdie & Slatyer 1976, Gill 1977).

Previous studies involving buried seed have generally found, as in this study, that there is very little correspondence between the buried seed pool and existing vegetation on the site (Oosting & Humphreys 1940, Donelan & Thompson 1980, Major & Pyott 1966). The absence of buried seed from woody dominants (e.g. blueberry in this study) has been documented (Major & Pyott 1966, Donelan & Thompson 1980). The absence of blueberry and the scarcity of *Carex* seedlings seen in this study may be due to these species reproducing mainly by vegetative means.

The appearance of *Geranium bicknellii* following fire (Ahlgren 1960, Ohmann & Grigal 1979, Outcalt & White 1981, Abrams & Dickmann 1982) and other disturbances such as cultivation, building removal, and road construction (Ahlgren, pers. comm.) has been documented in the Lake States. On jack pine sites in northern lower Michigan, peak occurrence of geranium is restricted to the first year after fire; individuals of this species are rarely present on older burned sites. This pattern of geranium behavior, however, does not occur on all Lake States sites. For example, Ahlgren (1979c) reported that *G. bicknellii* occurred in 90% of his sample plots two years after an old-growth red pine stand in northeastern Minnesota was burned. Krefting & Ahlgren (1974), also working in northeastern Minnesota, found geranium in 27% of the plots surveyed on a 4-year-old burn.

Ahlgren (1979a-c) extracted buried seeds in soil samples from many sites of different forest types and burning histories, and consistently found geranium to be an important component. Interestingly, when Ahlgren (1979c) monitored seedling emergence from intact soil blocks collected from a 270 year-old red pine stand burned 3 years previously and from an adjacent unburned area, geranium appeared only from the burned soil. Ahlgren (1979a) also planted soil-extracted geranium seed in sterile greenhouse soil and obtained 30% germination.

These data are in contrast to our findings. In Ahlgren's experiments, no heat treatment was given to soil samples or soil extracted seed, yet the geranium seed germinated. In our experiments with buried seed, geranium germinated only in flats exposed to heat treatment. This was further substantiated when 3 of 6 unheated control flats from the 3-year and 35-year sites, which showed no geranium germination for 18 weeks, produced geranium seedlings after the soil was heated. Also, seeds extracted from bulk soil samples from the 3-year site showed 20% germination (37 seeds total) when heated to 90°C for 30 min., whereas no unheated seeds germinated (30 seeds total) (Abrams & Dickmann, unpubl.)

Geranium in Minnesota, in the field at least, does not require heat from fire for germination (Ahlgren, pers. comm.). The apparent heat requirement for geranium germination in northern lower Michigan suggests that ecotypic differences exist for this species.

SUMMARY: Geranium bicknellii dominates vegetative cover the first year after fire on many jack pine sites in northern lower Michigan, but in subsequent years it disappears. To test whether heat from fire was responsible for this behavior, experiments using seed buried in the soil of different aged jack pine sites were initiated. Germination of buried geranium seed only occurred in heated treatments from 3- and 35-year-old sites; unheated controls produced no

germinants. The apparent heat requirement for germination of buried geranium seed from sites in northern lower Michigan contrasts with other Lake States studies and suggests ecotypic

differences in germination behavior.

Unheated soil from the 35- and 55-year-old sites produced significantly greater numbers of grass germinants than did heated treatments. Many important members of the plant community recorded on each site did not produce germinants in this experiment, and several species that germinated from buried seed were not surveyed on the sites.

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REVIEW

ENDANGERED AND THREATENED PLANTS OF OHIO. Edited by Tom S. Cooperrider. Ohio Biological Survey Biological Notes No. 16. College of Biological Sciences, The Ohio State University, Columbus, Ohio 43210. 1983 ["1982"]. 92 pp. \$10.00 postpaid.

Here is a concisely documented, thorough account of present knowledge concerning plants at risk—or even considered to be probably extirpated—in Ohio. It is an excellent model, carefully done, for such regional catalogs. The historical background and many bibliographic references will make it useful beyond Ohio for data on many of the most interesting plants of the Great Lakes region. Lichens, bryophytes, and vascular plants are included, but no algae or fungi. Records since 1950 are generally considered "recent" and in the absence of these a taxon will eventually be considered extirpated in the state if intensive field work in the near future does not relocate it.

Some species, such as Dalibarda repens and Besseya bullii, are nearly as scarce in Michigan as in Ohio. On the other hand, many species which we take for granted as abundant elements of our aquatic and terrestrial vegetation are considered at least threatened in Ohio—a good illustration of the effects (sometimes combined) of more extensive impingement on "natural" sites and, inevitably, of different climates. For a few examples: Potamogeton gramineus, P. zosteriformis (and other species), Carex bebbii, C. trisperma, C. viridula, Juncus balticus, Clintonia borealis, Sarracenia purpurea, Drosera intermedia, Potentilla palustris, Rubus strigosus, Polygala paucifolia, Cornus canadensis, Pyrola secunda, Vaccinium myrtilloides, Menyanthes trifoliata, Melampyrum lineare, Linnaea borealis, and Campanula rotundifolia are all so widespread and common in Michigan that it comes as something of a shock to find them classed as threatened or even endangered in the state immediately to the south. The importance of state lists becomes obvious, and an excellent defense is presented for state criteria (rather than solely national ones) which reflect the "different problems and needs of conservationists, planners, and biologists at the state level. The identification of unique sites or unusual biological communities within our state is largely contingent upon the identification of their unusual component species. A state list offers greater resolution in determining priorities for management or protection."

Comparing statistics is also instructive. In Ohio, 196 vascular plants are listed as threatened, compared with 200 in Michigan. But 328 taxa of vascular plants are listed as endangered, including those considered probably or perhaps extirpated, while in Michigan we list 13 species as endangered plus 24 as presumed extirpated (though the latter are to be considered as threatened should they be rediscovered). Does Ohio truly have 25 times as many endangered species as Michigan, or have we been far more conservative in designating them?

An element of particular interest is those species especially characteristic of recently disturbed ground in northern Michigan. Of these, *Polygonum cilinode, Chenopodium capitatum, Geranium bicknellii*, and *Aralia hispida* are all considered endangered in Ohio (the latter two may be extirpated) while *Corydalis sempervirens* is threatened. Such discrepancies in status for plants which, at least with us, depend on bulldozers to maintain ample habitat, suggest a topic for research, to be approached with great caution, on the biological requirements for survival.

—E. G. Voss

RHIZOMNIUM GRACILE, A MOSS NEW TO MINNESOTA, WITH THE DISTRIBUTION OF RHIZOMNIUM IN THE STATE

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Rhizomnium gracile Kop. is a circumboreal species whose range has been recently discovered to extend to Finland and Norway (Bowers 1980). In North America this species has had a known extensive distribution across the subarctic and boreal zones of Canada and Alaska (Koponen 1973) with one locality in the conterminous United States from Alger Co., Michigan (Koponen 1973, Crum & Anderson 1981). A new locality is reported here from the Lost River Peatland, Koochiching Co., northern Minnesota (48°12′N, 94°20′W). Annotations of the Rhizomnium collections located at the University of Minnesota herbarium (MIN) indicate that only R. appalachianum Kop., R. magnifolium (Horik.) Kop., and R. punctatum var. chlorophyllosum (Kindb.) Kop. were previously known from Minnesota localities. Rhizomnium appalachianum and R. punctatum var. chlorophyllosum are the only species that Koponen (1973) mapped for Minnesota, although Crum & Anderson (1981) mentioned R. magnifolium and also R. pseudopunctatum (Bruch & Schimp.) Kop. as present in the state. In the Lost River Peatland R. pseudopunctatum was collected frequently with R. gracile. To clarify the distribution of the Rhizomnium species in Minnesota a map based on annotated specimens is presented (Fig. 1).

The North American distribution of *R. punctatum* var. chlorophyllosum and *R. appalachianum* is mainly eastern, and Minnesota is located at the western limit of their main ranges. Rhizomnium magnifolium and R. pseudopunctatum are amphi-continental, and the Minnesota localities are at the western edge of their eastern range on the continent. Rhizomnium gracile has its southermost extension at the Minnesota and Michigan localities. The three remaining North American Rhizomnium species are northern [R. andrewsianum (Steere) Kop.] or western [R. nudum (Britt. & Williams) Kop. and R. glabrescens (Kindb.) Kop. (Koponen 1973)].

Rhizomnium gracile (Figs. 2-6) is distinguished from R. punctatum var. chlorophyllosum, R. glabrescens, R. nudum, and R. andrewsianum by the presence of micronemata on the stem (Koponen 1973; Fig. 2). It is differentiated from the more closely related R. appalachianum, R. magnifolium, and R. pseudopunctatum by its small size, unistratose leaf border (Fig. 5), and in particular very short costa (Fig. 2, 3).

Rhizomnium gracile is found in poorly to moderately minerotrophic fens [pH 6.2–7.5, specific conductivity (K_{corr.}) 45–240 µScm⁻¹, Ca⁺⁺ concen-

¹Limnological Research Center Contribution 289.

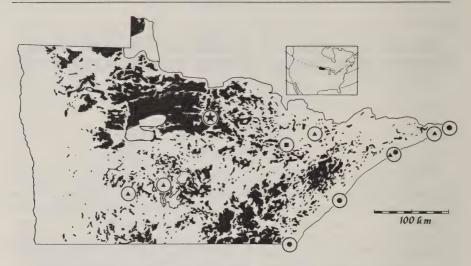


Fig. 1. Distribution of *Rhizomnium* in Minnesota. The map displays the major peatlands in the northern part of the state, north of Duluth (based on Malterer & Conway 1978). Lost River locality (\bigstar : R. gracile and R. pseudopunctatum); R. appalachianum (\blacktriangle); R. magnifolium (\blacksquare); R. punctatum var. chlorophyllosum (\bullet).

tration 17.9-22.2 ppm, and absorbance (at 320 nm) 0.360-0.670]² which contain a large variety of micro-habitats. Rhizomnium gracile is thus associated with an extensive bryophyte and vascular plant flora (up to 60 bryophytes and 28 vascular plants in some of the 20×20 m plots). The bryophytes having the most significant cover in the large relevés are Sphagnum magellanicum, Dicranum polysetum and D. undulatum, Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis, Polytrichum strictum, and Ptilidium pulcherrimum. The stand is dominated by Picea mariana in the overstory and Smilacina trifolia, Carex leptalea, C. gynocrates, Ledum groenlandicum, Carex trisperma, C. paupercula, Vaccinium vitis-idaea, and Linnaea borealis in the ground layer. Mire bryophytes that are less commonly found in northern Minnesota but present in plots containing R. gracile are Barbula fallax, Brotherella recurvans, Calliergon richardsonii, Campylium radicale, Conardia compacta, Dicranum ontariense, Rhizomnium pseudopunctatum, Rhytidiadelphus triquetrus, Tetraphis pellucida, Thuidium delicatulum var. radicans, Tomenthypnum falcifolium, Bazzania trilobata, Calypogeia fissa, C. integristipula, Frullania bolanderi, Geocalyx graveolens, Moerckia hibernica, and Odontoschisma denudatum. Rhizomnium gracile itself grows in small, strongly shaded micro-habitats on bare peat underneath Picea mariana and Thuja occidentalis, and there it is closely associated with Plagiomnium ellipticum, Pleurozium schreberi, Plagiothecium denticulatum, Lepidozia reptans, Brachythecium salebrosum, Hylocomium splendens, Cinclidium stygium, Hypnum lindbergii, H. pratense,

²The water-chemistry data are upper and lower observed limits for five samples. Absorbance or color is a relative indicator of water stagnation in the mire system. A value around 1.5 indicates highly stagnant water, such as in a raised bog. Lower values indicate higher flushing rates.



Fig. 2–6. *Rhizomnium gracile*. 2. Gametophore. 3. Small upper leaf. 4. Upper medial and marginal cells. 5. Transverse section through border. 6. Transverse section through costa at base of leaf.

Blepharostoma trichophyllum, Plagiochila asplenioides, Rhynchostegium serrulatum, Drepanocladus uncinatus, Lophocolea heterophylla, Riccardia latifrons, Lophozia rutheana, and depauperate populations of Sphagnum warnstorfii, Tomenthypnum nitens, Aulacomnium palustre, and Campylium stellatum.

Specimems examined (collected in Minnesota, located at MIN):

R. appalachianum. West base of Mt. Josephine, Grand Portage, Cook Co., Holzinger, Aug. 14, 1902; Itasca, Clearwater Co., Newcomb, July 29, 1941; Little Sletten Lake, St. Louis Co., Olson 597; Pike Bay Lake, Cass Co., Sharp, Aug. 22, 1971; Musci Acro. Bor.-Amer. 148, Grand Portage, Holzinger, July 14, 1904.

R. gracile Lost River, Koochiching Co., Janssens 8985, 10026, 10121, 10148, 10225, 10282, 10287, 10349.

R. magnifolium. Vermillion Lake, St. Louis Co., Arthur 180A.

R. punctatum var. chlorophyllosum. Grand Marais, Cook Co., Holzinger, July 16–Aug. 7, 1902; Susie Island, Cook Co., Olson 685a; Thompson (= Thomson), Holzinger, June 1891; Porcupine Ridge, Lake Co., Kellner, July 17, 1956.

R. pseudopunctatum. Lost River, Koochiching Co., Janssens 8945, 8971A, 10005,

10016, 10028, 10224, 10240.

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PUBLICATIONS OF INTEREST

- FLORA OF ICELAND. By Áskell Löve. Almenna Bókafélagid, Reykjavík. 1983. 403 pp. \$20.00. For those with a fondness for northern plants, this is a very attractive little flora, slightly expanded from the author's original Icelandic version. The line drawings and several color plates are by the accomplished artist Dagny Tande Lid. There are not only illustrations but also keys and descriptions for all species, together with chromosome numbers as determined from Icelandic material. Visitors to Iceland, as well as residents, are fortunate to have available such an excellent manual, which will fit into a (large) pocket.
- INTERNATIONAL CODE OF BOTANICAL NOMENCLATURE Adopted by the Thirteenth International Botanical Congress, Sydney, August 1981. Prepared and edited by E. G. Voss, Chairman, and members of the Editorial Committee. Regnum Vegetabile Vol. 111. 1983. 472 pp. \$39.00 for members of IAPT; \$48.25 for others, postpaid in U.S. [may be ordered from Scientific Publications Office, New York Botanical Garden, Bronx, N.Y. 10458]. The latest Botanical Congress, held in Australia in 1981, accepted or referred to the Editorial Committee almost 100 proposals to amend the Code—besides additions to the lists of names conserved (and thus legitimized even though they are in violation of one or more rules and would otherwise have to be dropped or applied in a different way). The new edition of the Code incorporates these changes along with numerous editorial improvements. The usual French and German translations are provided, the Appendices listing conserved names are updated, and the index is completely redone.
- THE MACK LAKE FIRE. By Albert J. Simard, Donald A. Haines, Richard W. Blank, & John S. Frost. U.S. Dep. Agr. Forest Serv., North Central For. Exp. Sta. Genl. Tech. Rep. NC-83. 1983. 36 pp. [Available from N. C. Forest Experiment Station, 1992 Folwell Ave., St. Paul, Minnesota 55108.] Here is the "full story" of the famous (or infamous) fire near Mio, Michigan, which in its first six hours on May 5, 1980, took one life, destroyed 44 buildings, and burned 20,000 acres of (mostly jack pine) forest land, attaining a rate of spread as fast as 6–8 miles per hour. Weather data, maps, aerial photos, considerations of "fuel" (vegetation), and prediction of effects on jack pine reproduction help to provide a thorough picture. There is no suggestion that anyone familiar with conditions recommended against starting the "prescribed burn" scheduled for the day to improve warbler habitat—and which ran out of control.

GERMINATION OF PRAIRIE PLANTS UNDER AMBIENT AND CONTROLLED CONDITIONS, W

Babette Kis 6048 N. 114th St. Milwaukee, WI 53225

The percentage of germination of a homogeneous group of seeds depends on such factors as genotype, health of seed, and environmental requirements. In this study the germination of seeds from 42 species of prairie plants was tested under ambient and controlled conditions.

Collection, storage, and viability were standardized so that results would more accurately reflect the conditions required for germination. Several plants of each species to be tested were grown from seed sources listed in an appendix, below; seed produced was used in the germination tests. Seed was collected when ripe; all seed not immediately sown was cleaned, air-dried, and stored at 60–80°F from 1–9 months before use. Small lots of seed were tested for viability with tetrazolium. Only seed from lots with a minimum of 80% viability was sown.

Several procedures were followed in both ambient and controlled testing. Between 100 and 300 seeds of each species were sown for each test. Legumes were not inoculated before testing. Ambient test conditions for local seeds were similar in soil type, pH, and moisture to nearby remnant prairies. Growing conditions for western seeds were obtained from the seed suppliers. Germination of seeds sown in Tests 1 and 2 was monitored from May to September. Air temperature, water, soil, pH, and light were controlled in Tests 3 through 8. Air temperature was maintained between 60 and 72°F, except as shown on the germination charts. Seeds were watered or misted as needed to keep the soil moist. The soil mix was composed of equal parts of unsterilized peat moss, perlite, topsoil, and vermiculite; the pH was 6.5. Seeds were placed on top of the soil mix and pressed into the soil. Flats of seed were placed under fluorescent gro-lites for 12–16 hours per day. Germination was monitored for five months from the day of seeding.

DESCRIPTION OF TESTS

- Test 1. Seed sown outdoors when ripe on prepared seedbeds with 2 exceptions: Castilleja coccinea and Gentiana andrewsii were sown in a 1-year stand of prairie grasses.
 - Test 2. Seed stored over winter at 60-72°F, then sown in late May or early June.
 - Test 3. Seed given cold treatment (dry stratified) for 8 weeks before sowing.
 - Test 4. Seed given cold treatment (dry stratified) for 12 weeks before sowing.
- Test 5. Seed placed in a solution of 1:100 to 1:500 parts GA to water for 24 hours before sowing.
 - Test 6. Seed placed in distilled water for 7 days before sowing.
 - Test 7. Seed moist chilled (stratified) for 8 weeks before sowing.
 - Test 8. Seed moist chilled (stratified) for 12 weeks before sowing.

Oenothera biennis

Potentilla arguta

Ratibida pinnata

Sylphium laciniatum

S. terebinthinaceum

Solidago nemoralis

Veronicastrum virginicum

Salvia pitcheri

Senecio aurea

Zizia aurea

Parthenium integrifolium

Petalostemum purpureum

GERMINATION PERCENTAGES

1 1 1 1 1 1 1 1 1 1 1 1	2	3	4	5			
Anemone cylindrica 45 A. patens 38 Aquilegia canadensis 38 Asclepias tuberosa 4 A. sullivantii 30 Aster ericoides 30 A. laevis 30 A. novae-angliae 20 Baptisia leucantha 19 B. leucophaea 3				3	6	7	8
A. patens Aquilegia canadensis Asclepias tuberosa A. sullivantii Aster ericoides A. laevis A. novae-angliae Baptisia leucantha B. leucophaea 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3		20	50				
A. patens Aquilegia canadensis 38 Asclepias tuberosa 4 A. sullivantii *** Aster ericoides 30 A. laevis 30 A. novae-angliae 20 Baptisia leucantha 19 B. leucophaea 3	0	0		0	0		92
Asclepias tuberosa 4 A. sullivantii Aster ericoides A. laevis 30 A. novae-angliae 20 Baptisia leucantha 19 B. leucophaea 3	73	46		50			
A. sullivantii Aster ericoides A. laevis 30 A. novae-angliae 20 Baptisia leucantha 19 B. leucophaea 3	0 +		37	90			71
Aster ericoides A. laevis 30 A. novae-angliae 20 Baptisia leucantha 19 B. leucophaea 3	12 +	20	45	70+	70		68
A. laevis 30 A. novae-angliae 20 Baptisia leucantha 19 B. leucophaea 3				29			28
A. novae-angliae 20 Baptisia leucantha 19 B. leucophaea 3						33	
Baptisia leucantha 19 B. leucophaea 3							
Baptisia leucantha 19 B. leucophaea 3						82	
B. leucophaea 3	0			20			
•	0			3			
				35			
Castilleja coccinea 0	0	0	0	0			
Coreopsis lanceolata 25	21	28	31	91			
C. palmata 7	0	0	18	71			
Desmodium canadense 22							
Dodecatheon meadii 0	0	0	0	0	0	20	48
Echinacea pallida	26			71			
E. purpurea 54	50	48		95			65
Eryngium yuccifolium 30*			78*	40*			
Gentiana andrewsii 3	0	0	0	0		27	87
G. crinita 15	0	0	0			0	
G. lutea 0	0	0	0	0		0	22
Geum triflorum 56	20	20		20			30
Heuchera richardsonii	4	14		44			23
Liatris pycnostachya 25	4+		38	60+			
Lithospermum canescens 13	0	0	0	0		0,00	12
Lupinus perennis 25	0			32		1.00	_
L. polyphyllus 29	5+		10	30			30
Monarda fistulosa 39							

42

41

45

28

39

80

30

9

8

15

30

27

45

31*

40*

89

0

79

20

40

91

90

0

58

CONCLUSIONS

Categories of seed response to germination tests may be determined for several species:

⁺Germination percentages varied with time of year.

^{*} Germination began slowly, and percentage of seeds germinating increased when temperature was raised to 78°F.

Category 1. Seeds germinated under a wide range of conditions; percentage of seed germinating varied with test method used. Examples: Coreopsis lanceolata, Asclepias tuberosa, Aquilegia canadensis, Heuchera richardsonii, Monarda fistulosa, Echinacea purpurea. GA appeared to positively effect germination of several of these species.

Category 2. Seeds germinated under external (ambient) conditions or moist stratification only. Examples: *Dodecatheon meadii*, *Anemone cylindrica*, *Gentiana andrewsii*, *Gentiana lutea*, *Lithospermum canescens*. GA

appeared to have no effect upon the germination of these species.

After-ripening appears to have been a factor in germinating several species, including *Liatris pycnostachya* and *A. tuberosa*. Additional tests of these species, conducted at predetermined intervals, may clarify the effect of after-ripening.

Current and future germination tests, to be incorporated in an updated report, may provide additional categories of germination response.

APPENDIX

Sources of seeds are as follows:

Minneapolis, MN

Lupinus polyphyllus

Barnes Prairie, Racine Co., WI

Allium cernuum Anemone cylindrica Aquilegia canadensis Asclepias tuberosa Aster ericoides A. laevis

A. novae-angliae

Baptisia leucantha B. leucophaea Desmodium canadense Dodecatheon meadii

Eryngium yuccifolium Gentiana andrewsii

G. lutea
Geum triflorum

Chiwaukee Prairie, Kenosha Co., WI

Asclepias sullivantii Castilleja coccinea Coreopsis palmata

SE Wisconsin Prairie Remnant, Dane Co., WI

Anemone patens v. wolfgangiana Besseya bullii

Northern Illinois Prairie Remnant, Lake Co., IL Coreopsis lanceolata

Murdock, NE

Echinacea purpurea Salvia azurea (Pitcheri) Heuchera richardsonii Liatris pycnostachya Lithospermum canescens Monarda fistulosa Oenothera biennis Parthenium integrifolium Petalostemum purpureum Potentilla arguta Ratibida pinnata Sylphium laciniatum S. terebinthinaceum Solidago nemoralis Senecio aurea

Veronicastrum virginicum Zizia aurea

Gentiana crinita Lupinus perennis

Echinacea pallida

The January issue (Vol. 23, no. 1) was mailed January 27, 1984.

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On the cover: The University of Michigan Biological Station, 1909–84, in the dead of winter (1971), from a wood cut by A. Hungerford, courtesy of Jane Taylor. The Station is celebrating its Diamond Anniversary. 150 M.58 2 Cop/sta

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May, 1984



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Articles dealing with any phase of botany relating to the Upper Great Lakes Region may be sent to the editor in chief. In preparing manuscripts, authors are requested to follow our style and the suggestions in "Information for Authors" (Vol. 15, p. 238).

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ASCOCARP FORMATION BY MORCHELLA ANGUSTICEPS AFTER WILDFIRE

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Morel mushrooms are commonly associated with deciduous trees, old orchards, grassy clearings, or disturbed woodlands and often with wood ashes (Cole 1910; Miller 1972; Krieger 1967; Smith & Hesler 1963). German peasants, according to Hard (1908), once burned forests to insure an abundant crop of morels. Smith & Hesler (1963) reported *Morchella angusticeps* in "stupendous quantities" following a 1962 forest fire in Idaho, and *M. esculenta* has also been reported to fruit following fire (Krieger 1967; McKenney & Stuntz 1971; Smith & Hesler 1963; Sturgis 1905).

This paper reports the prolific occurrence of *Morchella angusticeps* on exposed mineral soil following fire in a mixed coniferous forest in Cook Co., Minnesota. Ascocarps first appeared about 15 May 1977 and reached peak abundance in June, in a 400 ha. area burned 21–28 August the preceding year.

Fire has been an important natural disturbance in the Upper Great Lakes region for at least five centuries (Maissurow 1941), with severe fire years, during which large areas of forest were burned, occurring several times each century (Heinselman 1973). Most plants in early stages of succession are adapted to regenerate after wildfire (Ahlgren 1960).

The forest community on the study site originated ater a 1903 wildfire (Heinselman 1973). Apfelbaum & Haney (1981) described the forest before and after a 1976 fire (Fig. 1, 2.) An inventory of the vegetation had been compiled in May 1976; no ascocarps of *Morchella* were found there or in 12 comparable inventories of unburned forests nearby. In August of the same year, fire burned over the site which was studied again on 20–23 May, 16–18 June, and 9–15 July 1977, with additional observations made on 3 June and 17–20 June 1978, 15–20 May 1979, and 25–28 May 1983.

All but a few isolated areas in the immediate study area were burned. Ahlgren (1960) defined *severe burns* as those in which all litter, duff, and humus are consumed with only fire-killed snags remaining. By this criterion, 80% of the inventoried community were burned severely. *Hard burns*, according to Ahlgren, result when all litter and duff are ignited, but tree crowns are only scorched. In the study area, aspen in draws and a few jack



Fig. 1. The mixed jack pine and black spruce forest in 1976 before it was burned. Note the extensive bryophyte cover on the forest floor. Fig. 2. The same area after fire in June 1977 shows heavy tree mortality, exposed mineral soil covered with ash, and scattered sprouts of fireweed that were not present before the fire.

pine associations received a hard burn. Other aspen draw associations received only a *light burn* which resulted in loss of loose litter but little damage to the canopy.

Based on foliage appearance, nearly 60% of the trees were dead or dying in June 1977; by June 1978, 80% of the original stems were dead. Total cover by herbs, aspen root sprouts, and seedlings of jack pine and aspen was 28% in June 1976, before the fire, and 51% in July 1977. Bryophyte cover, however, decreased from 83% in 1976 to 14% in 1977. Not found before the fire but abundant in the burned forest were two ascomycete genera, *Pyronema* (two or three unidentified species) and *Morchella* (*M. angusticeps*).

No M. angusticeps ascocarps were found before the fire, but in the following year, on 20–23 May 1977, a few dozen were located in the burned site. By 16 June 1977, ascocarps were abundant throughout the burned area, averaging just over 15 per 100 m² in areas that had received a light to hard burn and under 2 per 100 m² in areas severely burned. On the same day, extensive effort was made to locate M. angusticeps in adjacent unburned forests, but none was found. On 9 July 1977, a survey revealed no remaining ascocarps. In June 1978, two visits were made to determine the status of

ascocarp production; only three were found after hours of searching. No evidence of *M. angusticeps* was found in May 1979, although *Pyronema* ascocarps were still abundant. In May 1983, no *Pyronema* or *Morchella* ascocarps were found. Complete absence of ascocarps in adjacent, unburned forest provided strong evidence that fruiting is related to fire. (A casual search of another recently burned area in June 1979 revealed a scattered occurrence of *M. angusticeps* on a site 35 km northwest of the area described here.)

From our observations and reports in the literature (Moser 1949; Peterson 1970; Ebert 1958; Sturgis 1905; Persoon 1818; Smith & Hesler 1963), there can be little doubt that both *M. angusticeps* and *M. esculenta* are commonly associated with fire or wood ashes; both species, however, also fruit regularly in other environments. By far the most apparent environmental effects of fire are neutralization of organic acids (Ahlgren & Ahlgren 1965), removal of potentially inhibiting species (Wicklow & Hirschfield 1979; Wicklow 1975), and removal of litter and decomposition products that might interfere with ascocarp formation.

Acid media are less suitable for *M. esculenta* and *M. crassipes* (Robbins & Hervey, 1959). Brock (1951) found better growth of *M. esculenta* in a basic medium containing sodium nitrate, although no single factor was related to mycelial growth. These findings are in agreement with Fron (1905) on mycelial growth under laboratory conditions. Because attempts to stimulate ascocarp production of *Morchella* in the laboratory have rarely been successful, the relevance of laboratory studies on mycelial growth to ascocarp production (and particularly in the field) cannot be evaluated. Peterson (1970), however, reported that liming unburned coniferous forest plots in Denmark resulted in the appearance of ascocarps of some genera other than *Morchella*; he found morels inconsistenlty related to fire.

Antibiotic interactions between ascomycetes have been well established (Wicklow, 1975; Wicklow & Hirschfield 1979). Removal of some species, or at least reduction in their growth, may permit growth of other fungi previously inhibited (Wicklow, 1975). Widden & Parkinson (1975), however, reported a water soluble inhibitor in burned but not in unburned litter. Nevertheless, they found that some species consistently develop in soil after fire, while others are apparently eliminated.

Our observations suggest that *M. angusticeps* occurred in a vegetative state in the unburned forest. Because the fungus was extensively established by June following the fire, as indicated by ascocarp presence, either mycelia or spores from previous seasons were already present at the time of the fire. Although spore production might have occurred in autumn following the fire (Sturgis 1905), *Morchella* typically fruits in May and June in the Great Lakes area (Smith & Helser 1963). It seems likely that the reduced occurrence of *Morchella* ascocarps in the severely burned areas stemmed from destruction of spores or mycelia by more intense fire. Unless spores are long-lived in the soil and unless they germinated to give rise to vigorous mycelial development between the September fire and the June fruiting period, mycelia must have been widespread before the fire. In either case, the formation of ascocarps

was triggered by the fire. Ascocarp development was not restricted to a few sites but was fairly consistent throughout the 400 ha. burn, varying only with fire intensity.

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CAREX PRAEGRACILIS: A HALOPHYTIC SEDGE NATURALIZED IN OHIO

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Carex praegracilis W. Boott ranges over a wide area of western North America from central Mexico to the Yukon. It is common in a variety of moist, exposed situations throughout this region. Although the species occurs as far east as Oklahoma, Missouri, and northern Michigan, the eastern limit of indigenous populations is uncertain (Fernald 1950; Gleason & Cronquist 1963; Mackenzie 1931). In recent decades C. praegracilis has been found as an adventive in southeastern Michigan and Ontario.

The eastward expansion of *Carex praegracilis* appears directly related to the use of road de-icing salts. This species was first collected in northwestern Ontario in 1961, southern Ontario in 1973 (Reznicek et al. 1976), and southeastern Michigan in 1965 (A. Reznicek, pers. comm., 1983). Once recognized, it was found to be locally common along the verges of major highways on soils of extreme salinity.

In 1976 this writer observed thick, circular clumps of a peculiar sedge along Interstate 75 in northwestern Ohio between Bowling Green and Findlay. Close mowing of the roadsides prevented the formation of fertile material, frustrating identification. These mysterious tussocks now are known to be *Carex praegracilis*. The first Ohio collection of *C. praegracilis* was in 1980 from a construction site in the city of Fairborn, Greene County (*Weishaupt s.n.*, OS 152068). This population subsequently has been destroyed (C. Weishaupt, pers. comm., 1983). This species, not listed for the state by Braun (1967) or Weishaupt (1971), was first attributed to the Ohio flora by Cusick (1982, 1983). Collections of *C. praegracilis* have now been made in 20 Ohio counties (Fig. 1). The sedge is particularly common in northwestern Ohio along Interstate 75.

The habitat is strikingly uniform. Carex praegracilis forms deep-rooted clones on the verges of major highways where road de-icing salt is applied repeatedly. Through time salt concentrations reach high levels which few species can tolerate. The associates of C. praegracilis in this desert-like habitat include Anagallis arvensis, Poa compressa, Puccinellia distans, Spergularia marina, and S. media. Not all of these species occur together at every site, of course. There is seldom much diversity at any one occurrence of these halophytes. The most constant associate of C. praegracilis is Puccinellia distans. These halophytic species also occur in similar associations with the Michigan and Ontario populations of C. praegracilis (Catling & Mackay 1980; Reznicek 1980). The verge community forms a prominent band adjacent to the highway pavement. Where a broad or deep median



FIG. 1. Carex praegracilis, Ohio county distribution, 1983, based on specimens at CLM, DAO, KE, MICH, MU, and OS.

separates traffic lanes, C. praegracilis generally will be found on the upper or outer edges of the median, not in the center or lower sections.

On rare occasions, *Carex praegracilis* grows on railroad embankments (Reznicek et al. 1976; Voss 1972). Only one such Ohio population is presently known. At this site in Cuyahoga County the associated species are similar to those in verge habitats.

Since Carex praegracilis is so widespread in Ohio, it must have become established well before the date of its first collection. How did this species escape detection for so long? The answer probably lies equally with the nature of the habitat and the plant itself.

Most botanists neglect the verge community where collecting can be dangerous and frequently unrewarding. The mowing of roadside "weeds" to a few inches in height distorts the growth forms of plants and may render species almost unidentifiable. Many of the species in this habitat are prominent only during their blooming periods and are otherwise easily overlooked.

Carex praegracilis is one of only two dioecious Ohio carices. The other is C. sterilis, a fen species not at all similar in other respects to C. praegracilis (Mackenzie 1931; Reznicek & Ball 1980). The dioecious character makes

this species difficult to identify since most keys fail to include leads for staminate plants. Carex praegracilis is also strongly dimorphic in growth habit. The staminate clones are short in stature and quite showy when in bloom due to exserted yellow stamens. The fertile culms of pistillate clones elongate greatly when mature, but are not especially distinctive. The perigynia are largely hidden by the pistillate scales and thus the infructescences at first glance appear immature. Roadside mowing drastically alters the aspect of the species. Mature pistillate specimens often are difficult to collect in identifiable condition. The blooming and fruiting period in Ohio is late May through June. At other times, C. praegracilis may easily be overlooked or ignored. Given sufficient familiarity, however, the eye can pick out the thick, leafy tussocks in the verge community.

Carex praegracilis has frequently been mistaken for two other Ohio carices, C. foenea and C. sartwellii. These two indigenous sedges are found in different habitats, but they superficially resemble pistillate plants of C. praegracilis. Using the keys to Ohio carices in Braun (1967) and Weishaupt (1971), pistillate specimens of C. praegracilis will key readily to one of these two species. The staminate plants cannot be identified at all using these manuals. Reznicek et al. (1976) provides an excellent key separating these three sedges.

The origin of the eastern populations of Carex praegracilis is an intriguing problem. Though apparently native in western Missouri, this species was reported from railroad yards in St. Louis in 1959 (Steyermark, 1963). The rail and highway connections between Missouri and the Great Lakes region are an obvious corridor for plant migrations. However, C. praegracilis was collected in the Upper Peninsula of Michigan as early as 1915 and 1934 (Voss, 1972). Although C. praegracilis is generally considered non-indigenous in the Great Lakes region, the possibility of its being native to northern Michigan cannot be wholly discounted. These early collections, from Keweenaw and Schoolcraft Counties, are not from rail yards or other obviously artificial sites but from moist openings and sandy depressions among jack pines. Perhaps the Great Lakes populations of Carex praegracilis are derived from more than one source.

The achenes of *C. praegracilis* may be carried in mud or other debris attached to trucks and construction equipment or as a contaminant in rail cargo. The strong air currents along highways doubtless contribute to the short-range expansion of established populations. Construction of the nation's interstate highway system may well have accelerated the rate of expansion of this and other halophytic species.

The future of *Carex praegracilis* in Ohio is probably bright. The species is well-established in its specialized habitat. The continued use of road deicing salts insures the permanence of that habitat and also creates new situations for colonization. *C. praegracilis* should not be viewed negatively. The tussocks create a hardy and attractive ground cover on otherwise barren roadsides. The salt tolerance of *C. praegracilis* might be exploited for highway beautification and control of soil erosion (Catling & McKay 1980; Reznicek et al., 1976).

The spread of this species and other halophytes is a virtual certainty. Plants of the verge community flourish in a newly-created habitat which few indigenous species can colonize. *Carex praegracilis* has become a significant member of the spontaneous vascular flora in Ohio and, possibly, throughout the Great Lakes region.

Specimens used in this study are housed at the following herbaria: CLM, DAO, KE, MICH, MU, and OS. I thank the curators at these institutions for courtesy and assistance. My special thanks are given to the following individuals for advice and information: David Brandenburg, Univ. of Oklahoma; Paul M. Catling, Univ. of Toronto: A. A. Reznicek, Univ. of Michigan; and Clara Weishaupt, Ohio State Univ. My research was supported by the Ohio Dept. of Natural Resources, Division of Natural Areas and Preserves.

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THE GENUS DICHANTHELIUM (POACEAE) IN MICHIGAN

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Dichanthelium is the largest all-native genus of grasses in Michigan. Originally treated as a subgenus of Panicum by Hitchcock & Chase (1910), some members of the complex were first elevated to generic status by Gould (1974). The most recent treatment of the group is a revision of the taxa of the United States and Canada by Gould & Clark (1978). The treatment presented here attempts to clarify specific limits within the complex in Michigan.

Although typically panicoid in both vegetative and floral characteristics and obviously closely related to *Panicum*, the genus is perhaps less closely related to Panicum than some other members of the tribe Paniceae common in Michigan, e.g., Setaria, Echinochloa, or Paspalum. Those familiar with Dichanthelium probably recognize most species in the field by relatively broad culm leaves or a dense cluster of basal rosette leaves which become conspicuous in late summer and autumn. Dichanthelium, however, differs as a group from other panicoids by its complex seasonal flowering and branching habit, viz., the early spring production of a simple culm terminated by a panicle (the vernal phase) which, in most species, produces little or no viable seed, followed by a variably complex proliferation of axillary branches (the aestival phase) bearing reduced, largely cleistogamous panicles. The latter apparently produce most of the viable seed in most species. In addition, all Dichanthelia are perennial, and most produce a basal rosette of winter-green (hiemal) leaves. In general, the hiemal leaves are shorter and relatively broader than culm leaves of either vernal or aestival phases and usually firmer in texture. In essence, the plants present three distinctive aspects depending on time of year. Both the aestival and hiemal aspects vary considerably in degree of development within local populations. For example, the rosette size or the number, position, and complexity of aestival branches appear to be influenced by site conditions and/or climatic conditions during the growing season, as well as genetic attributes of individual plants. Consequently, neither the aestival nor hiemal characteristics are, with few exceptions, of critical value in species delimitation.

Two other important features in which *Dichanthelium* and *Panicum* differ are physiological and cytogenetic. All *Dichanthelia* are non-Kranz (C_3) , whereas *Panicum* as currently treated contains both Kranz (C_4) and

¹This developmental stage is widely referred to as the "autumnal." However, it commences upon the maturation of the primary panicle during the late spring or early summer, hence aestival seems a more appropriate term.

²For a thorough discussion of Kranz and non-Kranz characteristics, see Brown (1977).

non-Kranz species (Brown & Smith, 1975), although most *Panicum* species in Michigan, as elsewhere, are C_4 . In the field these differences are expressed in earlier phenologies and, to a lesser degree, greater shade tolerance in *Dichanthelium* than in *Panicum* (with the possible exception of *P. verrucosum*, an annual C_3 species reported from Michigan but not observed in the course of this study).

Cytogenetically, most *Panicum* species form either polyploid or polyploid-aneuploid series, whereas most of the *Dichanthelium* species examined have been diploid, with some species represented by tetraploid populations.

Although the reproductive biology in *Dichanthelium* has not been thoroughly investigated, studies of one species complex indicate that most viable seed is produced through self-pollination (Spellenberg 1975a, b). Observations made during the course of this study suggest that this is true for the majority of the Michigan species.

Fully formed caryopses are commonly found in spikelets which have included or partially exserted stigmas but included stamens or, in some cases, apparently rudimentary stamens. Such a variable breeding system, coupled with largely cleistogamous aestival inflorescences, points toward a high degree of self-fertilization and a resultant promotion of unique, localized phenotypes. This has also tended to promote taxonomic confusion and a pro-

liferation of specific epithets.

Ecologically, *Dichanthelium* is confined, to a remarkable degree for so large a group of sympatric congeners, to similar habitats. It is not uncommon to find three, four, or more well-marked species within what would appear to be interactive (i.e., competitive) distances in uniform habitats. Most species are more or less confined to sands or sandy soils, mostly in drier portions of the soil-moisture drainage gradient. As a group, they are nearly absent from soils with moderate to high clay content and occur as components of open or sparsely populated communities. Although the reasons for this are not immediately apparent, one may be related to the architecture of the plant, which is generally poorly designed for effective competition in dense vegetation, or at least with sod-forming grasses. Shinners (1941) found the spatial distribution of some species in Wisconsin to be related to soil pH, most sites being circumneutral to acidic, as are the sands and sandy soils in Michigan.

Most of our *Dichanthelia* obviously profit from some degree of disturbance within the more mature communities in which they occur, e.g., creation of openings, trails, or burns in old or mature forest vegetation on appropriate soil types. Under such circumstances substantial increases in density have been noted where there were previously established residual populations. On the other hand, none of the species appears to be effective early colonizers and are rarely found in early secondary successional sites with extensive soil disturbance, although they are often found in long abandoned pastures and fields. For this reason they rarely occur under conditions where they would be considered "weeds," in sharp contrast to most other panicoid grasses in Michigan. Once established, the plants appear to be long-lived and the populations stable, as I have observed individual plants

and populations for at least 14 years and have detected no appreciable changes in vigor or size, respectively. These observations suggest that members of the genus as a whole were probably not abundant in presettlement times but were probably largely restricted to mature communities and that the present-day species' areas in the state have not been substantially altered by man's recent activities.

As originally monographed by Hitchcock & Chase, the Dichanthelium complex included over 100 species in North America north of Mexico; of those 34 species were attributed to Michigan. Subsequent treatments reduced the number somewhat; e.g., 25 species were included in the Michigan flora in Fernald's (1951) and also in Gleason & Cronquist's (1963) treatment. Voss (1972) recorded 21 species in the state, including one "problematic" species. Gould & Clark (1978) reduced the number to 26 species for North America and Canada, with 14 reported for Michigan. The treatment presented here recognizes the same number of species for the state (although the number differs in other respects). The substantial reduction in species number primarily results from placing a number of taxa recognized by others as species or varieties into synonymy and excluding putative hybrids from formal taxonomic status. The present treatment evolved from 14 years of extensive and intensive field observations throughout much of the northern portion of the range of Dichanthelium and extensive collecting in the Lower Peninsula of Michigan, especially during the summer of 1978.

As a whole, the genus demonstrates a remarkable degree of morphological similarity among species. This, of course, has been one of the major causes of taxonomic difficulty. With few exceptions, qualitative differences between species are few. For example, basic leaf shape is similar in all but two of the Michigan taxa, and inflorescence geometry, spikelet morphology, and indument type are essentially the same for all species. Consequently, quantitative features such as absolute values for overall plant size, leaf size, pubescence distribution, density and development, and allometric relationships among these and other variates are the most useful in characterizing individual taxa.

Data were obtained from mass (or population) collections, as well as herbarium specimens, in order to assess the range of variation of characters and determine the phenotypic structure of populations. These materials have been deposited in the Beal-Darlington Herbarium of Michigan State University (MSC). Additional information was obtained from specimens at the Cranbrook Institute of Science (BLH) and the University of Michigan (MICH).

All microstructure measurements were made with micrometer calipers or a dissecting microscope with an engraved stage. Macrostructure measurements were obtained with a standard metric ruler. Pubescence characterization, leaf lamina and sheath, internode and inflorescence dimensions were obtained at specified and standardized positions on the plant. Spikelet measurements were taken from various positions within the panicle in order to obtain the full range of sizes and, insofar as possible, from spikelets of vernal panicles. Culm and internode lengths were in all cases determined from mature primary culms, i.e., after initiation of aestival branching.

No attempt is made to present distribution data in other than general terms. During this study no new county records were obtained for species outside the expected range as deduced from the pattern of county records in Voss (1972).

8. D. commutatum

KEY TO SPECIES OF DICHANTHELIUM IN MICHIGAN

Α.	Leaf blades narrow, linear to linear-lanceolate, strict to narrowly ascending, the longest $\ge 20 \times$ longer than wide, mostly crowded toward culm bases; hiemal leaves reduced or wanting.
AA.	Leaf blades various, usually ≤15× longer than wide, if ≥20× longer than wide, not crowded near culm base, mostly distinctly cauline, variously ascending to widely spreading; hiemal leaves usually well developed. C B. Upper glume and sterile lemma exceeding and prolonged beyond fertile lemma forming a beak-like point; spikelets mostly ≥3.0(2.8–4) mm long. 1. D. depauperatum
	BB. Upper glume and sterile lemma ± equalling fertile lemma, if exceeding fertile lemma ± blunt or rounded, not beak-like; spikelets mostly <3 mm long. 2. D. linearifolium
C.	Largest vernal culm leaves ≥15 mm wide.
CC.	Largest vernal culm leaves ≤14 mm wide. G
	 D. Spikelets <2 mm long (1.3–1.9); plants glabrous except for spikelets and cilia of sheaths and laminae (if plants generally villous or pilose, go to couplet L). 14. D. sphaerocarpon
	DD. Spikelets >2.8 mm long.
Е.	Leaf sheaths glabrous to sparingly soft-pubescent, rarely papillose on ciliate margins. 7. D. latifolium
EE.	 Leaf sheaths variously papillose or papillose-pilose F. Larger leaves generally ≤2 cm wide, generally at least 10 × as long as wide; larger spikelets to 4 mm long, ± distinctly obovoid; primary panicle branches strict to narrowly ascending, panicle usually long-exserted; plants mostly <0.5 m high.
	3. D. xanthophysum FF. Larger leaves generally >2 cm wide, generally 6× or less as long as wide; larger spikelets usually ≤3.5 mm long, ovoid to ellipsoid; primary panicle branches ascending to spreading; panicle usually short-exserted or partially included in subtending leaf sheath; plants usually >0.5 m high at anthesis (up to 1 m or more). 6. D. clandestinum
G.	Larger spikelets ≥ 3 mm long (mostly 3.1–4).
GG.	Larger spikelets ≤2.9 mm long.
	J. Spikelets broadly ovoid to spheroid; lower glumes broadly ovate, mostly
	≤1.4(1-1.6) mm long. 4. D. oligosanthes JJ. Spikelets ± distinctly obovoid; lower glume narrowly ovate to lanceolate, mostly
K.	>1.7(1.6–2.1) mm long. K Spikelets sparingly short-pubescent to nearly glabrous; upper leaf surface glabrous to
KK.	sparingly pubescent. 3. D. xanthophysum Spikelets spreading-pilose or papillose-pilose with hairs to 2 mm long; leaf blades
	appressed-pilose. 5. D. leibergii
	L. Terminal leaf (flag leaf) and second and third leaves of vernal culms subequal in length (flag leaf usually at least 0.85 the length of the second, often longer than the third leaf); plants generally glabrous to sparingly and finely pubescent on lower sheaths and internodes; primary culm leaves ascending to widely spreading and ±
	horizontal at anthesis.
	LL. Flag leaf distinctly shorter than second and third leaves of primary culm (usually
	less than 0.75 as long as the second leaf); upper leaves of primary culm strict to narrowly ascending (sometimes spreading in shade grown plants); plants variously
14	pubescent, glabrate or glabrous.
M.	Leaf bases cordate, usually papillate-ciliate; ligule nearly obsolete to 0.5 mm long; spikelets mostly ≥2.2 mm long, glabrous to sparingly pubescent; fertile lemma usually applead by second alumn and sterile lemma.

MM. Leaf bases rounded or tapering at base, sometimes papillate-ciliate; ligule a fringe of hairs up to 1 mm long; spikelets mostly ≤2.1 mm long, glabrous to sparingly pubescent, often with the fertile lemma exceeding upper glume and sterile lemma. N

enclosed by second glume and sterile lemma.

- Largest leaf blades mostly <6 mm wide; primary culm leaves usually ± horizontal; spikelets mostly glabrous; lower glume usually ≥0.33 the length of the spikelet. 9. D. dichotomum
- NN. Largest leaf blades mostly ≥6 mm wide; primary culm leaves usually at least weakly ascending; spikelets sparingly and regularly pubescent; lower glume usually ≤ 0.25 length of the spikelet. 10. D. boreale
- Primary panicle long-exserted at anthesis; flagleaf borne ± midway between the culm Ο. base and the tip of the panicle (except sometimes in shade-grown plants); plants mostly glabrous; ligule obsolete or nearly so; hiemal leaves (and often lower culm leaves) with a distinct whitish, thickened margin; panicle branches often viscid; spikelets ± spheroid. 14. D. sphaerocarpon
- Primary panicle not conspicuously long-exserted, or if so, plants distinctly to con-00. spicuously pubescent; flagleaf borne well above the mid-culm position (usually 0.65-0.75 above culm base); ligules various; leaf margin hardly or not at all thickened, or if so, lower internodes and sheaths densely puberulent; panicle branches not conspicuously viscid; spikelets ± distinctly ellipsoid to ovoid.

Spikelets generally ≥2 mm long.

0 PP. Spikelets generally ≤1.9 mm long.

Q. Pubescence of two types, a short puberulence mixed with and overtopped by long, spreading to ascending, pilose hairs of variable length and density; spikelets mostly 2.2–2.6 mm long; nodes usually conspicuously bearded.

QQ. Pubescence of a single type or plants glabrous.

Plants generally glabrous, sometimes papillose-pilose or villous (sparingly) on lowest sheaths and internodes; spikelets minutely pubescent, ellipsoid to ovoid; lower glume mostly ≤0.7 mm long, ovate, rounded or blunt at apex; ligule ≤ 1 mm long (mostly ≤ 0.5). 10. D. boreale

RR. Plants papillose-pilose with ascending or spreading hairs up to 3 mm long (or more), these most dense on middle sheaths and internodes; spikelets broadly ovoid to obovoid, pilose; lower glume 0.7–1 mm long, ovate-deltoid, acute to subacute at apex; ligules mostly >1 mm, up to 5 mm long. 11. D. acuminatum

Pubescence of 2 types, a short, crisp puberulence throughout the plant, usually becom-S. ing mixed with longer, appressed to ascending pilose hairs of variable density on lower sheaths and internodes; nodal annulus usually distinctly puberulent.

SS. Pubescence of 1 type, of pilose or papillose-pilose hairs of variable length and density (but of generally uniform length at a given position on the plant), or plants glabrous; nodal annulus usually glabrous, sometimes papillate.

Spikelets 1.5–1.9(2) mm long; lower glume 0.6–1 mm long, usually distinctly acute; panicles and upper culms crisp- to spreading-puberulent (sometimes glabrate), becoming mixed on middle and lower internodes and sheaths with longer, appressed to ascending hairs, these indistinctly or not at all papillose; laminae usually glabrous or long-pilose on margins. 12. D. sabulorum

TT. Spikelets 1.2-1.6(1.8) mm long; lower glume 0.4-0.6(0.7) mm long, variable, but usually rounded, lobed or blunt at apex; panicles and upper culms with crisp to spreading puberulence, often with longer, spreading, villous or pilose hairs, these increasing in density and length downward, often becoming distinctly papillose; leaves variously pilose on both surfaces, usually with strongly ascending hairs.

intergrade between nos. 11 & 12

Spikelets 1.3–2 mm long; lower glumes 0.3–0.6(0.7) mm long, usually rounded, blunt U. or lobed, often apiculate; pubescence, where present, of ± uniform length, usually distinctly papillose, at least on middle and lower sheaths and internodes; nodal annulus ± glabrous (sometimes papillate); leaves glabrous to pilose on 1 or both surfaces.

11. D. acuminatum

Spikelets 1.2–1.6 mm long; lower glumes 0.3–0.5(0.7) mm long, usually rounded, blunt or ± lobed, sometimes apiculate; pubescence distinctly bistratal, of appressed, ascending, or spreading, short and long, pilose or papillose-pilose hairs, this condition often restricted to zones immediately below the panicle and lower sheaths and internodes; nodal annulus often ± pilose or puberulent (sometimes glabrous); laminae pilose on both surfaces, often with strongly ascending hairs on upper surface

intergrade between nos. 11 & 12

- 1. Dichanthelium depauperatum (Muhl.) Gould—Culms densely tufted, mostly 1–4 dm tall, shorter than to exceeding the tips of the subtending leaves, glabrous to sparingly pubescent on the lower internodes; leaves linear to lanceolate, flat to involute, glabrous to villous or pilose; inflorescence relatively few-flowered, branches spreading to strictly ascending; spikelets ovoid, glabrous to sparingly pubescent, mostly 3–4 mm long, sterile lemma and upper glume drawn into a beak-like point, often exceeding the fertile lemma by as much as 1 mm, lower glume mostly 0.3–0.5 length of spikelet, rounded to broadly pointed (terminal spikelets not uncommonly 2-flowered); aestival inflorescences borne near the plant base, few-flowered. Throughout the state, mostly in dry sandy sites, open woods, pastures, and abandoned fields on sterile soils.
- 2. **Dichanthelium linearifolium** (Scribner) Gould—*Culms* densely tufted, mostly 1–4 dm tall, shorter than to exceeding the tips of the subtending leaves, branching mostly from the base, occasionally from middle and upper nodes, glabrous to densely pubescent; *leaves* narrowly linear-lanceolate, flat to slightly involute, glabrous to sparingly pubescent on both surfaces; *inflorescence* relatively many-flowered, branches spreading to ascending; *spikelets* ovoid, rounded at summit, mostly 2–3 mm long, pubescent, lower glume mostly <0.25 length of spikelet, usually rounded or blunt at apex; *aestival inflorescences* borne at lower- and mid-plant positions, few flowered. Similar in distribution and often associated with the preceding.

Hybridization between D. depauperatum and D. linearifolium is apparently not uncommon, producing a complex of intermediates. The taxa are distinguished chiefly on the basis of absolute spikelet size and shape of the upper glume and sterile lemma, these characters being closely correlated. Mature D. linearifolium spikelets are rounded or somewhat truncated at the summit and range toward the lower range of spikelet size for the complex (Fig. 1). In contrast, D. depauperatum spikelets are distinctly larger, with the upper glume and sterile lemma prolonged into a beak-like point beyond the fertile lemma. Within the limited range of their morphology, individual plants vary widely in height, extent to which the inflroescence is exserted beyond the uppermost leaves (Fig. 1) and vestiture. None of these latter characters are strongly correlated with spikelet size, although D. linearifolium averages somewhat taller and tends to branch more freely than D. depauperatum. Although frequently found in association, both taxa are commonly found in extensive populations apart from one another. Plants with similar morphology, but with spikelets that are intermediate in size, and often in shape, have been described as Panicum perlongum Nash. Such plants are only arbitrarily distinguishable from either D. linearifolium or D. depauperatum, and while they are apparently not uncommon (they may frequently be overlooked), I have never observed them in large or pure populations. Hence, they are treated here as hybrids between D. depauperatum and D. linearifolium.

- 3. **Dichanthelium xanthophysum** (A. Gray) Freckmann—*Culms* mostly 2.5–5 dm tall, glabrous to sparingly pubescent; *leaves* broadly lanceolate, mostly 10-15 cm long, 8-12 mm wide, glabrous, ciliate, flagleaf often larger than lower leaves, sheathes papillose-pilose to glabrous; *inflorescence* few-flowered, branches strict to weakly ascending; *spikelets* \pm obovoid, 3.2–4 mm long, pubescent, lower glume 0.3–0.5 the length of the spikelet, lanceolate; *aestival branches* usually few, from middle nodes.—Dry to mesic sandy or coarse soils in open woods, clearings, and natural openings; apparently restricted to north of the tension zone in Michigan. Although Gould & Clark (1978) stated that this species is found in prairies, it is not normally found in prairie sites in Michigan.
- 4. **Dichanthelium oligosanthes** (Schultes) Gould—*Culms* mostly 2–7 dm tall, densely pubescent to glabrous; *leaves* broadly lanceolate, mostly 5–10 cm long, 5–10 mm wide, glabrous to sparingly pubescent, flag leaf usually much shorter than lower leaves; *inflorescence* relatively many-flowered, branches ascending to spreading; *spikelets* broadly ovoid, mostly 3–3.8 mm long, lower glume ovate, mostly 0.2–0.3 length of spikelet; *aestival branching* mostly from middle and upper nodes, often dense.—Throughout the southern Lower Peninsula, less common north of the tension zone, in a wide variety of habitats. Common in abandoned fields, natural clearings, and open woods on sterile, sandy soils but also in prairie relicts on well-drained loams or sandy loams.

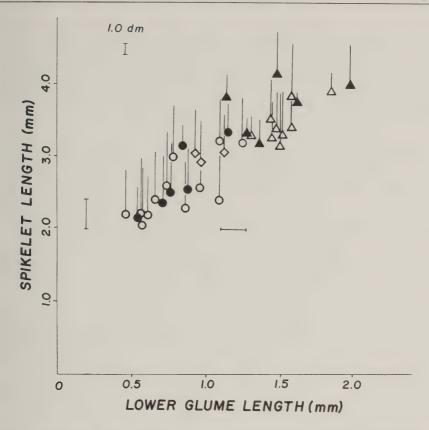


FIG. 1. Scatter diagram showing relationships among spikelet dimensions, plant height and primary inflorescence position in the D. linearifolium-D. depauperatum complex; \bigcirc —plants with spikelets rounded or blunt at apex; \triangle —plants with spikelets pointed or beak-like at apex; open symbols—plants with inflorescences exserted beyond leaf tips; closed symbols—plants with inflorescences equalling or shorter than tips of leaves; vertical bars on symbols—primary culm length (see scale); vertical and horizontal bars—3 standard errors of the mean of spikelet and glume lengths, respectively.

This rather variable, but generally distinctive species is distinguished from *D. leibergii* and *D. xanthophysum* by the shorter glume and/or vestiture characteristics of the spikelets. Two varieties have been reported for the state, the typical and the var. *scribnerianum* (Nash) Gould; however, there appears to be no clear differentiation among our plants.

5. **Dichanthelium leibergii** (Vasey) Freckmann—*Culms* mostly 3–7 dm tall, pilose at least below; *leaves* papillose-pilose, ciliate, mostly 8–25 cm long, 8–12 mm wide, flagleaf shorter than lower leaves, sheaths often densely spreading papillose-pilose; *inflorescence* relatively many-flowered, branches strict to weakly spreading; *spikelets* obovoid, conspicuously papillose-pilose, mostly 3–3.8 mm long, lower glume lanceolate, mostly 0.3–0.7 the length of the spikelet.—More or less restricted to dry to mesic, open sites south of the tension zone in Michigan, in prairie relicts and natural openings of dry, deciduous woods and former oak openings.

- 6. **Dichanthelium clandestinum** (L.) Gould—*Culms* robust, erect, often to 1 m or more tall, glabrous to papillose-hispid; *leaves* glabrous or scabrous, usually 15–25 cm long, 12–25 mm wide, ± cordate at base, lower sheaths papillose or papillose-hispid; *inflorescence* relatively short-exserted, often partially included in subtending leaf sheaths, branches ascending to weakly ascending; *spikelets* narrowly ovoid to ellipsoid, pubescent, mostly 2.8–3.2 mm long.—Mostly south of the tension zone in Michigan, primarily on mesic to moist sandy soils, not uncommonly in dense vegetation. Although not included in Michigan by Gould & Clark (1978), the species is common in the southern Lower Peninsula.
- 7. **Dichanthelium latifolium** (L.) Harvill—*Culms* stout and wiry, mostly 4–7 dm tall, glabrous to sparingly pubescent, nodes usually glabrous, sometimes loosely bearded; *leaves* glabrous, mostly 10–14 cm long, 30–40 mm wide, cordate, sheaths glabrous to pubescent, ciliate; *inflorescence* short- to long-exserted, rarely included in subtending leaf sheaths, branches spreading to ascending; *spikelets* narrowly to broadly ellipsoid to ovoid, mostly 3–3.5 mm long, glabrous to pubescent.—Common in dry to moist, usually sandy sites in open woods, borders, and clearings, frequent in gap-phase openings in mature woodlands, throughout the Lower Peninsula, apparently uncommon in the Upper Peninsula.

This is the commonest of the broad-leaved taxa in Michigan. While most of the materials I have examined are \pm glabrous throughout, occasional plants are variously pilose or villous on the lower sheaths and internodes and/or have bearded nodes and might key to *D. boscii* (Poiret) Gould & Clark in some treatments. However, both the morphological variation and ecological distribution appears to be continuous among these variants.

8. **Dichanthelium commutatum** (Schultes) Gould—*Culms* mostly 2–7 dm tall, slender, wiry, glabrous to pubescent, nodes glabrous to occasionally loosely bearded; *leaves* glabrous, mostly 4–7 cm long, 6–12 mm wide, papillate-ciliate on lower margins, \pm cordate, sheaths glabrous to pubescent, ciliate, flag leaf of primary culms often longer than lower leaves; *inflorescence* short- to long-exserted, branches ascending to spreading; *spikelets* narrowly ovoid to ellipsoid, mostly sparingly pubescent, sometimes glabrous, mostly 2.2–2.6 mm long.—Dry to mesic woods, forest borders, clearings, and natural openings, mainly south of the tension zone but occurring as far north as Oceana County in the Lower Peninsula.

This taxon, intermediate in appearance between *D. dichotomum* and *D. latifolium*, with a similar ecological distribution, frequently occurs with one or both of these species.

9. **Dichanthelium dichotomum** (L.) Gould—*Culms* slender, wiry, 1–7 dm tall, glabrous throughout or the lowermost sometimes sparingly pubescent, nodes glabrous to densely bearded; *leaves*, narrowly lanceolate, glabrous, sometimes sparingly ciliate on lower margins, mostly 3–8 cm long, 3–5 mm wide, flag leaf usually equal to or longer than lower leaves, usually ± horizontal, sheaths usually glabrous, sometimes lowermost pubescent; *inflorescences* short- to long-exserted, relatively few-flowered, branches mostly spreading to weakly ascending; *spikelets* ellipsoid to narrowly ovoid, mostly glabrous, fertile lemma often exceeding upper glume and sterile lemma, mostly 1.3–2 mm long, lower glume narrow, usually >0.3 the length of the spikelet; *aestival branching* highly variable, mostly from upper nodes. Common and widely distributed south of the tension zone in Michigan in dry to mesic woods, clearings, and natural openings along streams and lakes, mostly on sandy soils. Throughout the southern Lower Peninsula, generally south of the tension zone, but extending at least to Oceana County (*fide* Tim Mustard) and perhaps to Osceola County on the western side of the state.

Michigan materials range from delicate, slender plants typical of populations growing in mature woodland habitats, to more robust, freely branching plants typical of recently disturbed sites such as gap-phase openings in mature woods. Though generally glabrous, some plants or whole populations may range from sparingly pubescent to densely bearded on the middle and lower nodes. Plants extreme in the latter character often possess spikelets in the lower size range for the species and have been referred to *Panicum microcarpon* Muhl.; however, there is a wide range of variation in the nodal bearding character, and it does not appear to be correlated strongly with any other variate.

10. **Dichanthelium boreale** (Nash) Freckmann—*Culms* slender, erect, 2–7 dm tall, glabrous throughout or sparingly pilose to papillose-pilose below, nodes glabrous to sparingly bearded; *leaves* lanceolate, glabrous or sparingly pubescent, sometimes ± cordate at base, mostly 4–12 cm long, 5–10 mm wide, flag leaf shorter than lower leaves, ascending, sheaths glabrous to sparingly pilose or papillose-pilose, often ciliate; *inflorescence* long-exserted, relatively few-flowered, branches spreading to ascending; *spikelets* ellipsoid, sparingly pubescent, mostly 1.9–2.2 mm long, lower glume broad, mostly <0.25 the length of the spikelet, sterile lemma and upper glume ± equal to fertile lemma.—Widely distributed but apparently not common, in a variety of habitats, primarily in moist sandy or boggy sites, throughout the state.

A puzzling taxon, *D. boreale* is more or less intermediate in many respects between the *D. dichotomum* and *D. acuminatum* complexes. The relatively broader leaves, relatively short flag leaf which is usually strongly ascending, and pubescent spikelets distinguish the species from *D. dichotomum*. In addition, the two taxa occupy different habitats where they are sympatric in the state. In this respect, they display ecological differences similar to the two varieties of *Brachyeltrum* in Michigan (Stephenson 1971).

11. **Dichanthelium acuminatum** (Swartz) Gould & Clark. *Culms* highly variable, slender, 1–12 dm tall, ranging from glabrous to pilose or papillose-pilose throughout, nodes glabrous to densely bearded with appressed to ascending or spreading hairs, nodal sulcus usually glabrous or papillate; *leaves* usually scabrous to variously pilose on one or both surfaces, mostly 2–8 cm long, 1–7 mm wide, flagleaf strict to ascending, shorter than lower leaves, sheaths glabrous to densely papillose-pilose with appressed to spreading hairs to 5 mm long; *inflorescence* densely flowered, branches spreading to strictly ascending, glabrous to pilose; *spikelets* ovoid to ellipsoid, pubescent, mostly 1.3–2 mm long, lower glume usually broad, 0.25–0.4 as long as the spikelet.—Throughout the state in dry, sandy or coarse soils in open to dense woods, natural openings, abandoned pastures and fields, prairie relicts, fens, bogs, lake margins; throughout the eastern United States and southern Canada, westward to the Pacific coastal region and northern Mexico.

Members of the *D. acuminatum* complex are the most widely distributed and common representatives of the genus in Michigan. Local populations often differ markedly in appearance, ranging from short, compact, much-branched mat-like plants characteristic of open sites to tall plants with few sparingly branched culms characteristic of sites with dense vegetation. All these variations however, possess an indument of pilose or papillose-pilose hairs of esentially uniform length at a given position on the plant, although the pubescence may be primarily basal with the upper plant being glabrous. This vestiture condition coupled with small spikelet size, proportionally short, broad lower glumes and generally well-developed (often conspicuous) ligules are the most constant characters which tie the complex together.

Based on spikelet dimensions and pubescence length, most Michigan plants fall quite clearly into one of two general categories (Fig. 2). Shinners (1944) found a similar relationship between these characters in Wisconsin plants. Plants with a combination of long, usually spreading pilosity and spikelets in the upper size range for the species are referable to var. villosum (A. Gray) Gould & Clark. This taxon includes, among others, plants previously referred to Panicum praecocius Hitchcock & Chase. In my experience this variety is closely associated with prairie relicts in the state. Plants with shorter, ascending to spreading pilosity and spikelets in the lower size range for the species form a complex of intergrading phenotypes, many of which have been treated as distinct species or varieties. The majority of our plants fall between var. acuminatum and var. implicatum (Scribner) Gould & Clark, as treated by Gould & Clark (1978), and had been placed in Panicum implicatum Scribner by most previous authors. Glabrous plants or those in which the extent of pubescence is greatly reduced but which are otherwise indistinguishable from pilose plants have been referred to var. *lindheimeri* (Nash) Gould & Clark (= Panicum lindheimeri Nash). In view of the continuous variation between pubescent and glabrous plants and the absence of any apparent correlation of geographic distribution or habitat specificity with phenotypic variation, subdivision seems unwarranted. Hence, these small-flowered Michigan populations are collectively included here in var. implicatum.

A third variety (rare in Michigan), var. *densiflorum* (Rand & Redfield) Gould & Clark (= *Panicum spretum* Schultes) is known from a few widely scattered populations found in wet,

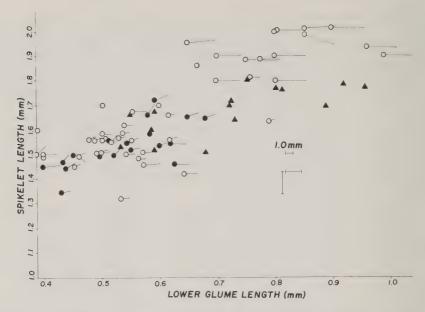


FIG. 2. Scatter diagram showing the relationships among spikelet dimensions and vestiture condition in the *D. acuminatum-D. sabulorum* complex. Vestiture character was determined on the first and second subterminal internodes and sheaths. —plants ranging from glabrous to pilose or papillose-pilose, referred in this treatment to *D. acuminatum*; —plants with bistratal vestiture (either bistratal pilosity or pilose and puberulent), considered as intergrades; —puberulent plants with or without longer appressed hairs at the stated position, referred in this treatment to *D. sabulorum*. Tails on symbols—length (see scale) and angle of attachment chairs. Vertical and horizontal bars—3 standard errors of the mean of spikelet and glumlengths, respectively.

sandy (acid), lake-shore habitats. It is primarily a coastal plain plant and in Michigan is often found with other coastal plain disjunct species. Plants of var. *densiflorum* are generally glabrous throughout and are readily distinguished from var. *implicatum* by the combination of longer and relatively narrower inflorescences, shorter spikelets, and generally taller stature (Table 1). In addition, var. *densiflorum* appears to be completely isolated ecologically from the other *Dichanthelia*.

Many Michigan plants are, to one degree or another, intermediate between D. acuminatum and D. sabulorum; these fit one or another description of several previously named taxa, but most fall well within the range of variation of *Panicum meridionale* Ashe. Some differ from D. acuminatum var. implicatum only by possession of a distinctly bistratal pubescence. Other specimens are distinguishable from D. sabulorum mainly on the basis of spikelet size and/or extent of pilosity (Fig. 2). Many of these plants are smaller and more delicate than most plants of either of the putative parent species (a point alluded to in some keys); however, the values for most characters are broadly overlapping (Table 1). Although Freckmann (1978) considered these plants to be of specific rank, primarily on the basis of fertility and habitat specificity, high fertility in inbred hybrid lines has been demonstrated by Spellenberg (1975) and would not seem to be a good criterion for establishing specific differentiation in at least some members of the genus. As for habitat specificity, I have never observed intermediate phenotypes in Michigan to occur in pure populations or unaccompanied by at least one of the putative parent species. Moreover, I have never observed these plants in what could normally be classified as mature communities; rather they are consistently found in variously aged successional sites resulting from moderate to severe habitat modification, the kind of conditions under which hybridization frequently occurs. A satisfying disposition for these phenotypes has been a

TABLE 1. Mean values of vegetative and floral characters of Michigan populations treated here as $Dichanthelium\ acuminatum\ var.\ villosum\ (1),\ D.\ a.\ var.\ densiflorum\ (2),\ D.\ a.\ var.\ implicatum\ (3),\ intergrades\ (4),\ D.\ sabulorum\ (5),\ and\ D.\ ovale\ (6).\ N=number\ of\ populations represented in sample. Estimates of dispersion are <math>\pm$ one standard deviation.

	Тахоп					
Variate	1	2	3	4	5	6
N	17	3	36	20	19	11
Culm length (cm)	39.3 ± 5.3	107.3 ± 18.5	53 2 = 16.7	30.3 = 6.2	35.6 ± 5.8	28.1 ± 3.1
Panicle length (cm)	4.8 ± 0.7	7.1 ± 2.4	4.7 ± 1.1	3.5 ± 0.7	4.0 ± 0.7	4.6 ± 0.8
Panicle width* (cm)	2.6 ± 0.4	2.8 = 1.1	2.6 ± 0.6	2 = 0.4	2.2 ± 0.4	2.7 ± 0.5
Terminal internode						
length (cm)	17.1 ± 3.8	32.4 ± 7.5	19.9 = 6.4	14.2 = 5.1	17.3 ± 49	15.4 ± 3.5
Flag-leaf length (cm)	46 ± 8.8	49.0 ± 19	34.8 = 14	24.4 ± 1.7	27.8 ± 7.9	36.6 ± 9.1
Flag-leaf width (cm)	4.3 ± 0.8	3 ± 1.1	3.6 ± 1.4	2.3 ± 0.2	2.9 ± 0.8	3.3 ± 0.8
Spikelet length (cm)	1.87 ± 0.11	1.46 ± 0.53	1.54 ± 0.10	1.52 ± 0.09	1.68 ± 0.09	2.42 ± 0.16
Lower glume length (cm)	0.78 ± 0.10	0.47 ± 0.05	0.54 ± 0.07	0.55 ± 0.09	0.72 = 0.12	1.07 - 0.08
Spikelet/lower glume	2.43 ± 0.36	3.11 = 0.27	2.87 ± 0.33	2.80 ± 0.37	2.38 ± 0.33	2.27 ± 0.17
Culm length/terminal						
internode length	2.28 ± 0.44	3.31 ± 0.35	2.67 ≈ 0.68	2.18 ± 0.43	2.07 ± 0.37	2.15 = 0.26

*length of lowest panicle branch.

long-standing problem, reflected in a variety of treatments of *Panicum meridionale* and allied taxa, e.g., Pohl (1947), Radford *et al.* (1968) and others previously cited.

12. **Dichanthelium sabulorum** (Lamarck) Gould & Clark. *Culms* slender, stiffly erect, mostly 1–3 dm tall, puberulent ± throughout, rarely glabrous, mostly with appressed-pilose hairs on lower internodes, often darkly pigmented, at least with age, nodes densely puberulent and/or appressed-pilose, nodal sulcus usually puberulent; *leaves* lanceolate, firm, mostly 3–6 cm long, 2–5 mm wide, mostly glabrous or puberulent on one or both surfaces, sometimes only ciliate near base, flagleaf strict, smaller than lower leaves, sheaths (at least the lower) puberulent and often pilose with appressed hairs: *inflorescence* long-exserted, densely flowered, branches spreading to ascending, puberulent to ± glabrous; *spikelets* pubescent, ovoid to ellipsoid, mostly 1.5–1.7 mm long, lower glume lanceolate, mostly 0.3–0.4 the length of the spikelet; *aestival branching* variable, mostly from middle and lower nodes.—Throughout the state on sandy and coarse soils, usually in dry sites in open woods, woodland borders and clearings, natural openings, and long-abandoned fields and pastures, less commonly under ± closed tree canopies or in dense, herbaceous or shrubby vegetation.

A precise delimitation is difficult because of the gradation with *D. acuminatum* previously discussed. Nonetheless, our plants are for the most part referable to *D. sabulorum* var. *thinium* (Hitchcock & Chase) Gould & Clark (= *Panicum columbianum* Scribner).

13. **Dichanthelium ovale** (Elliot) Gould & Clark. *Culms* slender, stiffly erect. 1–3 dm tall, puberulent ± throughout, rarely glabrous, mostly with dense pilosity at least on lower internodes, often darkly pigmented with age, at least the lower nodes usually prominently bearded with spreading hairs, nodal sulcus usually puberulent; *leaves* lanceolate, mostly 3–7 cm long, 3–8 mm wide, puberulent and/or pilose on 1 or both surfaces, rarely glabrous, flagleaf strict, sheaths puberulent and often pilose with appressed to spreading hairs: *inflorescence* long-exserted, relatively many-flowered, branches spreading to ascending, usually pilose; *spikelets* pubescent, ovoid to ellipsoid, mostly 2–2.6 mm long, lower glume mostly 0.3–0.5 as long as the spikelet; *aestival branching* mostly from middle and lower nodes.—Apparently confined to the Lower Peninsula, mainly in the western portion of the state, in dry, sandy soils or sands, in open woods and on stabilized dunes.

This and the preceding species, though similar in possessing a distinctly bistratal pubescence, are readily separated on the basis of spikelet dimensions (Table 1), as well as by the degree, attitude, and length of pilosity. Gould & Clark (1978) recognized two varieties, the typical and the var. *addisonii* (Nash) Gould & Clark, with only the former reported from Michigan. Our plants agree most closely with their description of the typical variety except for spikelet size, which is intermediate between the two. Most of the herbarium materials of Michigan plants that I have examined have been annotated by Voss as *Panicum commonsianum* var. *euchlamydeum* (Shinners) Pohl or by Shinners as *P. euchlamydeum*. Gould & Clark.

however, placed these names in synonymy under *D. sabulorum* var. *patulum* (Scribner & Merrill) Gould & Clark. Although these materials were apparently not examined by Gould or Clark, they in part formed the basis for Shinners' original circumscription of *Panicum euchlamydeum*. Pohl (1947), in reducing this entity to varietal status under *P. commonsianum* noted that the major difference between vars. *commonsianum* and *euchlamydeum* was the greater degree and density of pubescence in the latter. Voss (1972) noted the presence of the double ligule (ligule and pseudoligule) in our plants; this character is employed by Gould & Clark as a key character specifically for *Dichanthelium ovale*. Clearly then, the entity previously described as *Panicum euchlamydeum* by Shinners is misplaced in synonymy under *Dichanthelium sabulorum*.

14. **Dichanthelium sphaerocarpon** (Elliott) Gould. *Culms* slender, stiffly erect or spreading, 1–6 dm tall, mostly glabrous throughout; *leaves* firm, glabrous, ciliate or papillate-ciliate at base, mostly 4–8 cm long, 6–12 mm wide, hiemal and lower culm leaves often with a thickened, whitish margin, flagleaf usually much reduced relative to lower leaves, sheaths mostly glabrous, sometimes minutely puberulent, ciliate toward summit; *inflorescence* relatively densely flowered, long-exserted, often viscid; *spikelets* mostly minutely pubescent to glabrous, broadly ellipsoid, ovoid or spheroid, mostly 1.3–1.6 mm long, lower glume broadly deltoid, rounded or blunt, mostly 0.25–0.4 length of spikelet.—Dry to dry-mesic sites in open woods, clearings, and natural openings, mainly south of the tension zone in the state.

Of the 14 taxa considered as species in this treatment, 12 remain essentially unchanged from the definitions employed in the most recent formal treatment of the group in Michigan (Voss 1972), where they are included in Panicum. Definitions of the remaining two species, D. dichotomum and D. acuminatum, have been broadened to include variations recognized as distinct species by Voss and others. Three taxa recognized by Voss, Panicum perlongum Nash, P. meridionale Ashe, and P. calliphyllum Ashe, are excluded because of suspected hybrid origin. Although independently developed, the present treatment closely parallels, at least at the species level, that of Gould & Clark (1978), who recognized 14 species and six varieties from Michigan. Although the Gould & Clark revision contains some obvious discrepancies with respect to Michigan taxa, the nomenclature therein is employed in the present treatment. Among the most questionable aspects of the Gould & Clark treatment are the inclusion of Dichanthelium scoparium (Lamarck) Gould as occurring in Michigan, the exclusion of D. clandestinum, and the taxonomic treatment of the D. sabulorum-D. ovale complex.

Much of the confusion surrounding this genus has arisen from a high degree of variability in a relatively few species complexes, e.g., the Lanuginosa, Columbiana and Dichotoma groups of Hitchcock & Chase (1951). Although not extensively studied in *Dichanthelia*, clinal variation is marked in some groups within the genus (Spellenberg 1975b; Allred & Gould 1978) and has in the past prompted the recognition of variously localized populations as species or varieties. The recent trend has been to broaden species definitions in the genus as more detailed distributional and morphological data become available. As a consequence, attempts to delimit varieties within the context of such broadened species definitions inevitably result in some local or regional populations falling between or overlapping described varietal limits (e.g., Michigan populations in *D. acuminatum* or *D. sabulorum*). In addition, hybridization among a number of taxa occurs with varying

frequency in Michigan and has contributed further to the general taxonomic confusion. Most suspected hybrids are relatively infrequent, and their putative parents deduced with varying degrees of difficulty. These supposed hybrids occur mostly as single plants or small populations. However, apparently frequent hybridization occurs in several species, most notably between D. acuminatum and D. sabulorum and between D. depauperatum and D. linearifolium. In these cases, the extent to which the parent species were reproductively isolated in the past is problematic; there is little doubt, however, that hybridization between these species pairs has been facilitated by extensive post-settlement habitat modification. In this context, D. commutatum and D. ovale as recognized here also need further study.

I would like to thank John Beaman, Dept. of Botany and Plant Pathology, Michigan State University, for suggestions during the preparation of the manuscript and curators of the herbaria of the University of Michigan and the Cranbrook Institute of Science for making collections available.

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REVIEW

PROCEEDINGS OF THE EIGHTH NORTH AMERICAN PRAIRIE CONFERENCE. Edited by Richard Brewer. Department of Biology, Western Michigan University, Kalamazoo 49008. 1983. 176 pp. \$28.00 postpaid.

Kalamazoo, Michigan, was the site for the Eighth North American Prairie Conference, so it is not surprising that the host state is well represented in the papers presented. At least four articles in the present volume have a strong Michigan flavor, if not devoted entirely to prairies in the state. Included are reports on the Maxton plains of Drummond Island (Stephenson); absence of certain aquatic plants from the Prairie Peninsula, with many maps (Stuckey); composition of prairies in (and adjacent to) southern Michigan (Thompson); and Michigan cemetery prairies (C. Pleznac). Two papers deal with central and southern Ontario prairie sites. Several treat prairies in Illinois and Wisconsin. R. Pleznac argues convincingly that "reconstruction" is a more accurate word than "restoration" for the rebuilding of prairies, especially on sites that never supported them before. Other papers deal with such reconstructed prairies, and several consider uses of prairies and prairie plants, including educational and interpretive ventures. The volume concludes with abstracts of 33 papers presented at the conference but not among the 39 published in these proceedings. Except for the halftones (which are too coarsely screened), the printing is attractive. As with other proceedings in the series, there is much here for the prairie enthusiast, whatever his particular interest. -E. G. Voss

Publications of Interest

TIMBER RESOURCE OF MICHIGAN'S WESTERN UPPER PENINSULA, 1980. By John S. Spencer, Jr. U.S. Dep. Agr. Forest Serv., North Central For. Exp. Sta. Resource Bull. NC-60. 1983. 102 pp.—TIMBER RESOURCE OF MICHIGAN'S NORTHERN LOWER PENINSULA, 1980. By Pamela J. Jakes. Ibid. NC-62. 120 pp.—TIMBER RESOURCE OF MICHIGAN'S EASTERN UPPER PENINSULA, 1980. By W. Brad Smith. Ibid. NC-64. 103 pp.—TIMBER RESOURCE OF MICHIGAN'S SOUTHERN LOWER PENINSULA, 1980. By Jerold T. Hahn. Ibid. NC-66. 119 pp.* These four reports present vast amounts of data gathered in 1980 for the fourth forest survey of Michigan. There is much more information than in the slim report published in 1966 on the third survey; in this respect the present series resembles the full 15 reports issued 1948-1957 for the second survey, although there are now no generalized forest cover maps, a useful feature of the second survey. Highlights on forest area, timber volume, stand conditions, and timber use are in each report. It comes as something of a surprise to see Norway spruce and river birch listed among the "tree species groups" in the Upper Peninsula—and to discover that there are 665,000 board feet of Ohio buckeye sawtimber in the U.P. as well as 589,000 feet of eastern redcedar! Why black walnut and yellowpoplar are consistently listed in tables, though never with any figures after them, is another mystery involving trees that do not grow in the U.P. and doubtless explainable only by blaming a computer.—E. G. Voss

^{*}Available from N.C. Forest Experiment Station, 1992 Folwell Ave., St. Paul, Minn. 55108.

THE FLORA OF ROCK COUNTY, WISCONSIN:

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Since the publication of our original flora (Musselman et al., 1971), the authors as well as other botanists have continued field and herbarium studies on the plants of Rock County, which lies midway along the southern boundary of Wisconsin. Enough additions, corrections, and revisions have come to light to warrant publication of a supplement at this time. Since other important data will probably accrue as time goes on, a series of supplementary reports is envisioned.

Collections were made in all parts of Rock County. Particular attention was given to sites that yielded new county records at the time of our original investigations. These were mostly remnants of formerly large communities that now are utilized completely for agricultural purposes. Perhaps most interesting to us in this regard are areas having true prairie vegetation, whether they are situated on uplands or in lowlands subject to inundation. We give here three such examples. The grass marsh and open woods bordering the Rock River and the cooling canal for the power plant west of Hwy. 51 (collection site R2) are characterized by many of the most common yet, at the same time, most often ignored species of southern Wisconsin. Along with these species are others of greater biogeographic interest: Equisetum × litorale, Amorpha fruticosa, Hypericum sphaerocarpum, Sium suave, and Agastache nepetoides. Our one extant colony of Ruellia humilis occurs on a newly discovered prairie relic located alongside the industrial park on the east edge of Beloit (Q9). From this same disturbed dry prairie, which is totally surrounded by huge areas of cleared cropland and pastures, we also report another station for Ratibida columnaris. Plants previously recorded from Harmony Prairie (G2) include many species not found elsewhere in the county. Listed as new from this gravel-hill prairie, now doomed by subdivision for housing, are Carex umbellata and the Great Plains grass Muhlenbergia cuspidata, the latter usually associated in Wisconsin with the Mississippi River bluffs in the Driftless Area.

Several of the species added to the flora are introduced plants, as yet but slightly naturalized, which in the course of their migrations may not have reached the county until after 1971, such as *Dianthus armeria*, *Lotus corniculatus*, *Lythrum salicaria*, *Echium vulgare*, *Galeopsis tetrahit*, and *Carduus nutans*. Others, like the single clump of the lovely *Belamcanda chinensis*,

near the foot of a slope and invisible from the road, are no doubt long persistent garden escapes overlooked earlier. As in any flora, some of the native species initially missed are those that are infrequent or rare because they are disjunct from other regions, such as *Allium stellatum*, or are at the very edge of their geographic ranges, such as *Platanthera (Habenaria) hyperborea, Quercus coccinea, Agastache nepetoides*, and *Viburnum prunifolium*.

Many of the taxa reported in the authors' original flora (1971) have now been found at additional sites, but to elaborate every new record would require more space than could be justified for data of only very local interest. Most of the records that are included here fall into four categories: (1) species and hybrids newly recorded from Rock County; (2) species previously reported for which additional stations are of interest for some particular reason. e.g., one proposed for listing as "threatened" (Thr.) or "endangered" (End.) in Wisconsin, one generally known to be rare or local (Rol.) in the state, one observed to be changing its frequency in the area, etc.; (3) species formerly listed on the basis of unchecked reports and now verified by voucher specimens; and (4) species that should be deleted from the original list for reasons discussed below (cf. "Doubtful and Excluded Species"). Further additions or subtractions result from changes in taxonomic concepts since the publication of our flora. In cases of less well-collected species, additional data are reported if later observations and collections have shown them to be much more frequent or to occupy a much greater array of habitats than were previously documented. The combined catalogues now list a total of 1,167 species of indigenous (922 or 79%) and non-indigenous (245 or 21%) vascular plants, not including hybrids and infraspecific taxa. Of the indigenous group 49 species appeared in the annotated list of endangered and threatened higher plants of Wisconsin (Read, 1976).

Background information and bibliographic references have been presented earlier and need not be reviewed here except to call attention to a report on the vegetation of the Chamberlain Springs tract by Ward (1956). The format of the previous "Catalogue of Species" is followed in the present supplement, but more complete annotations are given for those taxa new to Wisconsin or particularly worthy of note. A few details need further explanation. An asterisk designates a plant not native to Rock County; a "+" indicates a species or hybrid until now unreported from Rock County. Most localities are identified by the symbols employed in the "Key to Collection Sites" of the original flora, and readers are referred to the detailed habitat descriptions found therein. Otherwise, township names and section numbers are given, if possible, or whatever information appears on labels. To the "Key to Collection Sites" may be added two new ones: Q8. CMStPP RR, W of Clinton (13, 21-24); Q9. Dry prairie along CMStPP RR, N of Colley Rd. (29). Because of their floristic interest, the areal description of the following sites is being enlarged by additions of sections: C1. (19 SW); G1. (28); K1. (29 SE); M1 (29 N); M8. (3 NW); S6. (35 NW); T4. (16W); T5. (34). At four of the sites, unusual species are limited largely to the following sections: D6. (11 E, 12 W); E5. (23 NW); N1. (17 SW, 18 NE); P7. (12).

The specimens examined for the supplement are deposited in (or have been distributed to) the following herbaria: University of Wisconsin Rock County Campus-Janesville (UWJ), University of Wisconsin-Madison (WIS), University of Wisconsin-Whitewater, Milwaukee Public Museum (MIL), Beloit College (BELC), University of Minnesota (MIN), the Field Museum of Natural History (F), the Morton Arboretum (MOR), and several others.

NEW TAXA AND ADDITIONAL LOCALITIES TO THE CATALOGUE OF SPECIES

LYCOPODIACEAE (Clubmoss Family)

+Lycopodium digitatum A. Br. (L. flabelliforme, L. complanatum f.). *Crowfoot clubmoss*. Dry oak woods, H1. The specimen previously reported as *L. complanatum* has been re-identified as this species. *L. complanatum* is not known south of the "Tension Zone" except from Waushara Co. (cf. Peck & Taylor 1980, map 68).

EQUISETACEAE (Horsetail Family)

Equisetum × ferrissii Clute (E. hyemale × E. laevigatum) (E. laevigatum of Tryon et al., 1953). *Ferriss' horsetail*. Railroads, Q8 R1 R2; dry to moist open or shaded fields, slopes, roadsides, and embankments.

+E. × litorale Kuhlw. (E. arvense × E. fluviatile). Shore horsetail. Shallow water, R2.

OPHIOGLOSSACEAE (Adder's Tongue Family)

Botrychium dissectum Spreng. f. obliquum (Muhl.) Fern. *Cut-leaved grapefern*. Wooded sandy or gravelly slopes, J1, Janesville 11. The collection earlier reported as *B. multi-fidum* actually represents a variant of *B. dissectum* with subentire pinnules.

POLYPODIACEAE (Polypody Family)

Cystopteris fragilis (L.) Bernh. var. mackayi Laws. *Mackay's fragile fern*. Rocky woods, R1. The collections from J1 and T7 previously included under this species have also been placed in var. *mackayi*. *C. fragilis* var. *fragilis* is confined to the northern half of Wisconsin (Peck & Taylor 1980, map 27).

+C. protrusa (Weath.) Blasdell (C. fragilis p.). Creeping fragile fern. Dolomite outcrop,

04; rich woods, Q1. This species was previously included under C. fragilis.

TYPHACEAE (Cat-tail Family)

Typha angustifolia L. *Narrow-leaved cat-tail*. Marsh, S6; roadside ditches. This cat-tail continues to spread in Wisconsin and may represent a formerly non-indigenous species immigrating northward. The earliest known specimens are from four general areas, Madison (1922–29), Milwaukee (1937–40), Green Bay (1939–41), and Fond du Lac (1941). Collections made over the next 20-year period came mainly from the eastern third of the state. Since about 1960 it has reached scattered localities beyond this region, as there are collections from Marinette, Marathon, and Douglas counties in the north and Monroe, Richland, and Lafayette counties in the west. Narrow-leaved cat-tail is now known from at least 22 counties (F, MIN, SUWS, UWSP, WIS).

+T. ×glauca Godr. (T. angustifolia × T. latifolia). Cat-tail. Marsh, A4.

NAJADACEAE (Pondweed Family)

*Potamogeton crispus L. Curly-leaved pondweed. Stream, Center 11 SW. In their "Preliminary Report" Ross & Calhoun (1951) mapped three isolated locations in Wisconsin for this introduced pondweed. Subsequent years of collection and observation have shown that *P. crispus* is steadily becoming more common, although it still seems to be restricted to southern and western parts of the state. See Stuckey (1979) for a detailed discussion of this species in North America.

+P. illinoensis Morong. Illinois pondweed. Lake, D7 (Moore, 1982, UWJ, WIS).

HYDROCHARITACEAE (Frog's-bit Family)

Elodea canadensis Michx. (Anacharis c.). Common waterweed. Slough, D1; brook, S5;

ditch, T5; lakes and ponds; frequent.

E. nuttallii (Planch.) St. John (Anacharis n.). *Slender waterweed*. Slough, T3. Infrequent in Wisconsin, where possibly declining due to habitat disturbance, but locally common in hard water in the southern part of the state.

+ Vallisneria americana Michx. Tape-grass. Lake Koshkonong (Stout, 1904, WIS).

GRAMINEAE (Grass Family)

+*Agrostis stolonifera L. Creeping bent. Moist grassy places. Var. stolonifera: 02. Var. palustris (Huds.) Farw. (A. palustris): T3 (Fell, 1957, WIS).

Cenchrus longispinus (Hack.) Fern. *Sandbur*. Railroad, M1; dry sandy ground, Newark 29 N, Newark 31; streetside, corner of Court and Franklin, Janesville.

+*Festuca arundinacea Schreb. *Tall fescue*. Sandy riverbank, Fulton 12 (*Pierce & Aronson*, 1967, WIS).

- F. octoflora Walt. (Vulpia o.). Six-weeks fescue. Open sandy banks, outcrops, prairies, oak woods. Var. glauca (Nutt.) Fern.: T7. Var. tenella (Willd.) Fern.: S4 T7. Intermediate between var. glauca and var. tenella: Avon 21 (Boebel & Laube, 1964, WIS).
- + Muhlenbergia cuspidata (Torr.) Rydb. *Prairie muhly*. Dry prairie, G2 (*Moran*, 1976, BELC).
- Panicum dichotomiflorum Michx. Fall panic grass. Roadsides, railroads, especially waste ground and cult. fields, D7 Q1, Fulton 12, Fulton 14; very common.
- +*P. miliaceum L. ssp. ruderale (Kitag.) Tzvel. (P. spontaneum). Wild proso millet. Solid stand on edge plus scattered plants in maize field, Milton 34 SE (Nee 21762, 1981, WIS); locally abundant in cultivated fields of Zea mays and Glycine max, where invariably associated with Setaria faberi, S. viridis, Panicum dichotomiflorum, and Abutilon theophrasti. This aggressive annual weed is rapidly spreading throughout the midwestern United States (North Dakota, South Dakota, Iowa, Minnesota, Wisconsin) and southern Canada (Ontario, Quebec). Although reported by Harvey (1979) as present in Wisconsin since about 1970, the first record from the state supported by voucher specimens was not obtained until H. H. Iltis collected wild proso millet in 1978 on the Messerschmidt farm, 1 mi. N of Truax Field in Dane Co. (Iltis 28456, WIS; Iltis 28456a, BELC, CAN, CHAPA, DAO, FLAS, GA, IA, IBUG, ISC, KY, MICH, MIL, MIN, MOR, NO, PH, TNS, UWL, UWM, WIS, and others). In addition to material from Dane and Rock counties, there are now specimens in WIS from Brown, Iowa, Jefferson, Fond du Lac, Green Lake, Richland, and Waukesha counties. Old reports (including those in Fassett, 1951) for P. miliaceum from Wisconsin should be referred to ssp. miliaceum.
- P. virgatum L. Switchgrass. Railroads, 12 L2 M1 R1. With us usually adventive along railroads, although a native plant in the region.
- + Paspalum ciliatifolium Michx. var. stramineum (Nash) Fern. *Lens grass*. Sandy ground, Avon 22 SW (*Fell*, 1957, UWJ, WIS).
- +*Poa annua L. Speargrass, annual bluegrass. Lawn weed, B1, Beloit 25 NE, Kellogg Ave., Janesville; common.
- *Setaria faberi Herrm. *Giant foxtail*. Roadsides, O4 Q1 S3. An apparent recent introduction to Wisconsin, this native of Asia has spread rapidly and has become an important weed of cultivated fields in the southern half of the state during the past 30 years. There are now numerous herbarium specimens from at least 19 counties (OSH, UWJ, WIS), the oldest collected in 1953 in eastern Iowa Co.
- +*Sorghum bicolor (L.) Moench. (S. vulgare). *Sorghum, broom-corn*. Roadside, Beloit 36 SW

CYPERACEAE (Sedge Family)

- + Carex cephaloidea (Dew.) Dew. Sedge. Rich woods, Q1 S8.
- C. cephalophora Muhl. *Woodbank sedge*. Moist meadow, O2; oak woods, jct. Hwy. 59 and Yahara River (*Ebert*, 1960, WIS); dry to moist woods, thickets, slopes, and banks.
- C. davisii Schw. & Torr. Davis' sedge. Beloit (Lathrop, s.d., WIS). (Rol.)
- C. foenea Willd. (C. siccata). *Hay sedge*. Dry to mesic prairies, L4 M1 P3, Rock 19 SE; open oak woods, S4 T1; dry, usually sandy open ground.

ssp. *ruderale*Culms mostly 2–8(12) dm tall; panicle mostly narrow and rather compact, usually lax or nodding, usually ± included at base, 6–31(45) cm long, much narrower than to half as broad as long, 1–15(20) cm wide; branches of panicle rigid, ascending to appressed, the pulvini scarcely developed; fertile floret light or dark tan to orange, somewhat shiny, persistent on panicle.

¹The following couplet will distinguish the two subspecies known from the region: Culms 7–21 dm tall; panicle open or only slightly contracted, erect, included at base until maturity, finally exserted, 9–48 cm long, about twice as long as wide, or shorter, 6–33 cm wide; branches of panicle slender, loosely ascending to spreading at flowering time, the pulvini well developed; fertile floret when mature dark grayish to brownish-black, very shiny, disarticulating (sometimes above the glumes and sterile lemma) from panicle.

- C. molesta Mack. Sedge. Low prairie, L2 (Schulenberg, Ciolac, & Swink, 1970, MOR); sedge meadow, F2; low roadsides, T6, Avon 34.
- C. tenera Dew. Sedge. Edges of woods, R1 S1; low, open ground, T6; dry to moist woods, openings, thickets, and fields.
- +C. trisperma Dew. Sedge. Sphagnum bog, E1.
- +C. umbellata Willd. Sedge. Eroded sandstone, J2; dry prairie, G2.
- + Cyperus odoratus L. var. squarrosus (Britt.) Gilly. *Tawny umbrella sedge*. Edge of marsh, 04.
- + Eleocharis compressa Sulliv. *Flat-stemmed spikerush*. Wet ditch, S6. (Det.: H. K. Svenson, 1973).
- E. erythropoda Steud. (E. calva). *Spikerush*. Wet ground, A4 B1 D3 D7 E1 E5 L2 O2 O4 O5 O6 P1 P5 P7 R1 S3 S7 T5, Avon 19 NE. Most material previously listed under *E. smallii* should be referred to *E. erythropoda*, the common *Eleocharis* in the region.
- E. smallii Britt. (E. palustris). *Small's spikerush*. Marshes, often in shallow water, A3 B1 T3, Avon 12 (*Fell*, 1957, WIS).
- + Eriophorum virginicum L. Tawny cotton-grass. Leatherleaf bog, A1.
- + Scirpus acutus × S. validus. *Bulrush*. Shallow water, Fulton 14 (*Smith*, 1967, University of Wisconsin-Whitewater).

LEMNACEAE (Duckweed Family)

- +Lemna turionifera Landolt. *Duckweed*. Pool in lowland forest, T3; open marsh, E1 (*Iltis*, 1969, WIS); small pond, Milton 6 SW (*Iltis & Janecek*, 1956, WIS); lakes, streams, and sloughs. These collections and numerous others from throughout Wisconsin were annotated by Landolt in 1981 as this newly described species.
- + Wolffia borealis (Engelm.) Landolt (W. punctata). Water-meal. Pool in lowland forest, T3; small pond, Milton 6 SW (Iltis & Janecek, 1956, WIS). (Both det.: E. Landolt, 1981.)

COMMELINACEAE (Spiderwort Family)

+*Commelina communis L. var. ludens (Miq.) C. B. Clarke. *Common day-flower*. Yard weed, Q1, Beloit 25; ditch, corner of Riverside and Briar, Beloit.

JUNCACEAE (Rush Family)

- + Juncus acuminatus Michx. *Sharp-fruited rush*. Marshy shore, A3. (Verif.: F. J. Hermann, 1979.) (Rol.) This specimen was previously listed as *J. nodosus*.
- + J. canadensis La Harpe. *Canadian rush*. Wet, sandy shore, without exact locality (*Haynie*, 1930, F).
- +J. interior Wieg. *Inland rush*. Sandy bank, Avon 21 (*Boebel & Laube*, 1964, WIS.) LILIACEAE (Lily Family)
 - + Allium burdickii (Hanes) Jones (A. tricoccum b.). Wild leek. Mesic upland woods, R1. (Det.: A. G. Jones, 1978.) Customarily this taxon has been included in A. tricoccum or treated as a variety of the latter, the two being so similar that the differences were not wholly understood (see Voss 1972, p. 412; Swink 1974, pp. 14–15). The problem was recently restudied by Jones (1979), who recognized it as a distinct species.
 - + A. stellatum Ker. Wild or prairie onion. Dry prairie, M1. (Rol.)

IRIDACEAE (Iris Family)

- +*Belamcanda chinensis (L.) DC. *Blackberry-lily*. Sandy bank, B2. Escaped from cult. ORCHIDACEAE (Orchid Family)
 - + Platanthera hyperborea (L.) Lindl. var. huronensis (Nutt.) Luer (Habenaria h. h.) *Tall* or *leafy northern bog orchid*. Springy thicket, O5.
 - + Spiranthes magnicamporum Sheviak. *Great Plains ladies' tresses*. Low prairie, L2. (Det.: C. J. Sheviak, 1974.) One collection reported in the Flora as *S. cernua* has been referred to this species, newly named by Sheviak (1973) and subsequently recognized by Luer (1975). Although not as frequent as true *S. cernua*, this species seems to be scattered throughout southern and western Wisconsin, characteristically in dry (usually) or moist calcareous prairies.

BETULACEAE (Birch Family)

Betula × sandbergii Britt. (B. papyrifera × B. pumila). Sandberg's birch. Low prairies, fens, S3 S6; wet woods, Avon 23; sedge meadows, shrub-carrs, and tamarack bogs. The collections from Newark Twp. originally labeled as B. pumila var. glandulifera seem

better referred to this hybrid, which is as common in southern Wisconsin as its dwarf parent.2

FAGACEAE (Beech Family)

+ Quercus × bebbiana Schneid. (Q. alba × Q. macrocarpa). White oak. Woods, Fulton (Watson, s.d., WIS). (Det.: J. W. Hardin, 1973).

+ O. coccinea Muenchh. Scarlet oak. Sugar River bottomland (Johnson s.n., 1971, WIS).

(Verif.: R. J. Jensen, 1975; examined also by W. R. Overlease, 1980.) The question of whether scarlet oak is really a member of the Wisconsin flora was reviewed at length by Wadmond (1933), who supposedly settled the matter when he wrote that "Q. coccinea did not occur in Wisconsin at all." Most botanists have accepted this conclusion, but a few others are convinced that the scarlet oak, as classically defined, should be maintained as an indigenous species in the state flora. A recent statement to this effect was published by Thomson in Fassett (1976, p. 126). Two earlier and hitherto unreported collections, both from low pastures in southern Wisconsin [Dane Co.: ca. 5 mi. E of Madison, 27 Sep 1954, Kuhlman s.n. (WIS). Dodge Co.: along Hwy. 28, 8 mi. NE of Horicon, 24 Sep 1966, Harshbarger s.n. (WIS)], have been identified as Q. coccinea by Jensen, even though in his account of subgenus Erythrobalanus (1977, p. 400) Wadmond's assertion is repeated. Overlease writes that the identities of all three collections are a little uncertain because all show some degree of intermediacy in morphological characters.

+ Q. × palaeolithicola Trel. (Q. ellipsoidalis × Q. velutina). Black oak. Dry woods, Janes-

ville 15 (Mori, 1965, WIS). (Det.: R. J. Jensen, 1975.)

ULMACEAE (Elm Family)

*Ulmus pumila L. Siberian elm. Hedgerow, R1; roadside, Newark 33 (Fell, 1957, WIS); edges of unused parking lots, Beloit 26 NE, Rock 1 SW. This weedy species had not been recorded as an escape in Wisconsin until 1956, when it was collected by Hartley near Onalaska, La Crosse Co. It is definitely increasing, especially in the waste ground of urban areas and along railroads.

MORACEAE (Mulberry Family)

Morus rubra L. Red mulberry. Quarries (Olds, 1893, WIS). (Rol.) All of the specimens passing under this name in the Flora belong to M. alba.

POLYGONACEAE (Buckwheat Family)

*Polygonum convolvulus L. Black bindweed. Yard weed, Q1; railroads, P3 Q8; gardens and other cult. or disturbed ground; common.

P. scandens L. False buckwheat. Damp open ground. Var. scandens: Magnolia 13 NE. Var. cristatum (Engelm. & Gray) G1.: Avon 29 W (Fell, 1957, WIS).

CHENOPODIACEAE (Goosefoot Family)

+ Chenopodium album var. lanceolatum × C. berlandieri var. zschackei. Lamb's quarters. Weed patch along dirt road, D1 (*Iltis & Janecek*, 1956, WIS). (Det.: H. A. Wahl, 1961.)

*Kochia scoparia (L.) Schrad. Summer-cypress. Railroad, M1; roadsides, O4, Fulton 28 (Thompson, 1965, WIS); dumps and waste ground; common.

*Salsola kali L. var. tenuifolia G. F. W. Mey. Russian thistle. Railroads, L2 P6 Q8 Q9.

AMARANTHACEAE (Amaranth Family)

Froelichia gracilis (Hook.) Moq. Cottonweed. CNW RR, Beloit (Shinners, 1942, WIS). PHYTOLACCACEAE (Pokeweed Family)

*Phytolacca americana L. Pokeweed. Edges of woods, Q1 Q3 Q5 Q9 S9. Rare or very local in southern Wisconsin where it occurs most frequently in Rock Co.

Caryophyllaceae (Pink Family)

+*Dianthus armeria L. Deptford pink. Old fields, S1 M2 M7.

²Betula pumila var. pumila is attributed in Gray's Manual (Fernald 1950, p. 536) to Wisconsin, in addition to var. glandulifera, but according to the Illustrated Flora (Gleason 1952, 2:36) and the Manual of Vascular Plants (Gleason & Cronquist 1963, p. 246) the typical variety (under B. pumila) ranges only as far west as Michigan. All material from Wisconsin in WIS and UWJ is var. glandulifera (young leaves and branchlets persistently glandular). True var. pumila (young leaves and branchlets without glands) does not seem to occur in the state.

RANUNCULACEAE (Crowfoot Family)

+Ranunculus flabellaris Raf. × R. sceleratus L. *Crowfoot*. Flooded field, Hwy. N, 3 mi. W of Whitewater (*Smith* 3858, 1966, WIS). (Verif.: L. Benson, 1978.) Evidently the first report of this crowfoot hybrid in the literature, although the parent species, both of which were found growing with it, are widespread.

Thalictrum revolutum DC. var. glandulosius Boivin. Waxy meadow rue. Brookside, Turtle

31 S. (Thr.)

CRUCIFERAE (Mustard Family)

+*Alliaria officinalis Andrz. (A. petiolata). *Garlic mustard*. Shaded lawn, Turtle 30 S. Arabis canadensis L. *Sicklepod*. Woods, O1 P3. The specimen earlier listed from O4 is *A. laevigata*.

A. divaricarpa Nels. *Rock cress*. Railroad embankment, P3; streamside, P7; gravelly or sandy soil. The specimen reported in the Flora from A1 is *A. glabra*.

*Hesperis matronalis L. *Dame's rocket*. Roadsides, fields, open woods, E1 N3 O6 R1, Beloit 26 NE.

*Rorippa austriaca (Crantz) Bess. *Austrian field cress*. Low fields, waste places, Q1 Q7, Beloit 36 E (*Dawe*, 1971, BELC), Turtle 31 W (*Munger*, 1967, BELC). First reported from Wisconsin by Small in 1923 and subsequently listed for the state in the standard manuals for our region, but excluded from the Wisconsin flora by Patman & Iltis (1961). Present collections and field observations indicate that the species is persisting and either spreading slightly or being occasionally re-introduced in the south-central sector of the state. It is known from Dane, Rock, and Walworth counties.

PLATANACEAE (Plane-tree Family)

Platanus occidentalis L. *Sycamore*. Floodplain along Rock River, Rock 22 NW. (Thr.) Very local in southern Wisconsin along the Rock, Sugar, and lower Wisconsin rivers.

FABACEAE (Bean Family)

Lespedeza leptostachya Engelm. *Prairie bush clover*. Disturbed dry prairie, M2 (*Moran s.n.*, 1975, BELC). (End.) This species, once presumed extinct in Wisconsin, seems to have been maintaining itself, albeit precariously, as it has been collected at least five times since 1969. It is now known from eight counties. (See also Tans & Read 1975, p. 138.)

+*Lotus corniculatus L. *Bird's-foot trefoil*. Pasture, Bradford 19 SW; roadside, Beloit 10 NE. Introduced as a cover crop in recent decades and slowly establishing itself as a weed

of fields, roadsides, and waste ground.

RUTACEAE (Rue Family)
Ptelea trifoliata L. *Hop tree*. Thickets, Q8, Rock 3 SE. (End.)

POLYGALACEAE (Milkwort Family)

Polygala polygama Walt. var. obtusata Chodat. Purple milkwort. Dry prairie, M2.

EUPHORBIACEAE (Spurge Family)

Chamaesyce nutans (Lag.) Small (Euphorbia preslii). Eyebane. Railroads, D1 D2 P3 Q8; disturbed lawn, Beloit 35 E; very common.

*Euphorbia cyparissias L. Cypress spurge. Eroded sandstone, J2; roadsides, S6, Newark 26 SW. Although long established throughout Wisconsin, this garden weed seems to be slowly declining in our area.

*E. esula L. (E. podperae³). *Leafy spurge, wolf s-milk.* Roadside, O1; dry streambed, 03. This Eurasian weed has increased noticeably in our area in recent times.

+*Poinsettia dentata (Michx.) K1. & Gke. (Euphorbia d.). *Toothed spurge*. Railroad, P3; roadsides, M2, Beloit 10 SE, Beloit 36 NW. Possibly native in southwestern Wisconsin, but introduced here.

HIPPOCASTANACEAE (Horse-chestnut Family)

*Aesculus glabra Willd. *Ohio buckeye*. Low woods, R1. Curtis (1950, pp. 157, 529) implies that this species is indigenous in our region although its range is usually considered to lie

³According to Croizat (1945), the North American populations included in this species properly belong to *E. virgata* Waldst. & Kit. and *E. ×intercedens* Podp., entities closely related to if not conspecific with *E. esula*. Richardson (1968) calls our material *E. podperae* Croiz. (*E. ×intercedens*), but we prefer for now to use the more conventional epithet.

south of Wisconsin. It is probable that his specimens, which were taken in a bottomland forest along the Yahara River near Fulton, came from an escaped tree. Other collections made in Wisconsin show the species to be rarely spreading from cultivation. It is known in addition from Grant, La Crosse, Milwaukee, Richland, and Vernon counties.

HYPERICACEAE (St. John's-wort Family)

Hypericum sphaerocarpum Michx. *Round-fruited St. John's-wort*. Low prairie, R2. (Thr.) All Wisconsin records are from moist prairies along the Rock and Sugar rivers in Rock and Green counties.

LYTHRACEAE (Loosestrife Family)

+*Lythrum salicaria L. *Purple loosestrife*. Streambank, Spring Brook, La Prairie 6. Stuckey (1980) recently published an account of the introduction and spread of this species in North America.

ONAGRACEAE (Evening Primrose Family)

Gaura biennis L. *Gaura*. Railroads, P3, Turtle 29 C; gravelly field, Turtle 6 SW; roadside, Center 2 SW. Rare and scattered in southern Wisconsin except for Rock, Green, and Walworth counties, where locally frequent.

+*Oenothera nuttallii Sweet. White-stemmed evening primrose. Disturbed dry prairie, M1 (Moran, 1975, BELC). Possibly native, but more likely adventive from farther west.

+O. oakesiana (Gray) Robbins. *Evening primrose*. Railroads, A3 P3. (Both det.: W. Dietrich, 1981.)

O. villosa Thunb. (O. strigosa). Evening primrose. Railroad ballast, P5, Union 16 NW; fenceline, N3; roadside, S3 (Fell, 1957, WIS).

ARALIACEAE (Ginseng Family)

+*Aralia spinosa L. Hercules' club. Roadside, H5. Escaped from cult.

UMBELLIFERAE (Parsley Family)

Berula erecta (Huds.) Cov. var. incisum (Torr.) Cronq. *Water parsnip*. Springs, O5. (Rol.) ERICACEAE (Heath Family)

+ Vaccinium angustifolium Ait. var. laevifolium House. Low sweet or early sweet blueberry. Open sandy woods, L1.

PRIMULACEAE (Primrose Family)

Androsace occidentalis Pursh. Rock jasmine. Lawn weed, Q1. (Rol.)

ASCLEPIADACEAE (Milkweed Family)

Asclepias sullivantii Engelm. Prairie milkweed. Low prairie, P5. (End.)

BORAGINACEAE (Borage Family)

+*Echium vulgare L. Blueweed. Railroad, R1.

Hackelia virginiana (L.) Johnst. *Beggar's lice*, *stickseed*. Dry to mesic woods, J1 R1 Q1 T7, Beloit 26 NE.

Onosmodium molle Michx. ssp. hispidissimum (Mack.) Cochrane. False gromwell, marbleseed. O3 (Wadmond, 1906, MIN); Beloit (Olds, 1895, BELC); dry open ground, Palmer Park, Janesville (Mori & Kallunki, 1974, WIS). (Thr.) Two of these specimens were cited by Cochrane (1975); see also his disussion (1976) of the O. molle complex.

VERBENACEAE (Vervain Family)

Verbena × moechina Moldenke (V. simplex × V. stricta) *Vervain*. Roadside, abandoned gravel pit, Newark 36 NE (*Souter & Rice*, 1972, BELC, UWJ; *Tans*, 1975, WIS). These collections, the only records for Wisconsin, were cited by Tans & Iltis (1979).

LABIATAE (Mint Family)

+ Agastache nepetoides (L.) Ktze. Yellow giant hyssop. Open woods, R1 R2. (Thr.)

+*Galeopsis tetrahit L. Hemp-nettle. Low field, O2.

Scutellaria parvula Michx. var. parvula. *Small skullcap*. Sandstone bluff, T2; railroad, 6 mi. N of Beloit (*Anthoney*, 1933, WIS); Beloit (*Beloit Coll. Sci. Assoc.*, *s.d.*, WIS). (End.) SOLANACEAE (Nightshade Family)

+*Datura stramonium L. *Jimson weed*. Roadsides, Q1, Beloit 25 NE; cult. field, Turtle 31 W; cemetery dump, Turtle 30 SW; barnyards.

SCROPHULARIACEAE (Figwort Family)

+ Agalinis purpurea (L.) Pennell var. borealis Pennell (Gerardia p. parviflora, G. pauper-cula). *Purple false foxglove*. Sedge meadow, E1. Reported on the original list as *A. tenuifolia*, but the specimen seems better referred here on the basis of stouter pedicels and longer calyx lobes.

Lindernia dubia (L.) Pennell (incl. var. riparia). False pimpernel. Drainage ditch, S6. The only Rock Co. specimen originally labeled as Gratiola neglecta is actually L. dubia.

Mimulus glabratus HBK. ssp. fremontii (Benth.) Pennell. Yellow monkey flower. Spring, O5, locally abundant. (Rol.)

+*Penstemon gracilis Nutt. ssp. gracilis. *Slender beard tongue*. Gravel-hill prairie, abandoned gravel pit, M7. Introduced from farther west.

ACANTHACEAE (Acanthus Family)

Ruellia humilis Nutt. Wild petunia. Dry prairie, Q9 (Moran, 1975, BELC). (End.)

CAPRIFOLIACEAE (Honeysuckle Family)

*Lonicera × bella Zabel (L. morrowi × L. tatarica) *Honeysuckle*. Disturbed woods, thickets, G2, Union 7, Magnolia 10 NW, Beloit 26 NE; common.

Symphoricarpos occidentalis Hook. Wolfberry. Railroad ballast, E4 L2 O5 Q8.

- + Viburnum prunifolium L. *Black haw*. Bottomland woods (oak-ash), T3 (*Wood, Nelson, & Diekelmann s.n.*, 1981, WIS), a single large clone. (End.) This species is extremely rare in Wisconsin, where it reaches the very westernmost edge of its range at the present station. Salamun (1979, p. 109) states that he examined material from only Milwaukee and Racine counties. There are other records from the counties of Kenosha (*Schulenberg s.n.*, 1972, MOR) and Ozaukee (*Iltis 21801*, 1963, MIN).
- V. rafinesquianum Schult. *Downy arrow-wood*. Mesic to dry open woods. Var. rafinesquianum: Q3. Var. affine (Bush) House: C3, Avon 31 (*Fell*, 1957, WIS). The collections from C3 and O1 labelled "V. dentatum var. lucidum" and reported as such are actually V. rafinesquianum, not an uncommon species in the region. However, another collection, Musselman 3786 (UWJ, WIS), apparently represents an escaped shrub and supports our record of V. dentatum (sensu lato, including, as Gleason evidently does, V. recognitum) from Rock Co. Better material has been collected in Walworth Co.: common in rich woods, 2 mi. W of Genoa City, 10 Jun 1973, Linderud 150 (WIS; verif.: E. G. Voss, 1981). Although neither the usual manuals nor the recent treatment by Salamun (1979) includes Wisconsin in the range of V. dentatum, it appears to belong on the list of the state flora.

DIPSACACEAE (Teasel Family)

+*Dipsacus fullonum L. (D. sylvestris). *Common teasel*. Cemetery dump, Turtle 30 SW. The specimen originally listed under *D. laciniatus* can be better referred to this species (see Salamun & Cochrane 1974, p. 257).

*D. laciniatus L. Cut-leaved teasel. Roadside, 1 mi. E of Indianford (Greene, 1947, WIS; Curtis, Greene, & Sauer, 1954, WIS).

CAMPANULACEAE (Harebell Family)

Campanula aparinoides Pursh. *Marsh bellflower*. Wet meadows, marshes. Var. aparinoides: D3 T6. Var. grandiflora Holz. (C. uliginosa): E1 E4 J4 O2 R2 S1.

COMPOSITAE (Composite Family)

Artemisia serrata Nutt. Sawtooth sagebrush. Wet prairies, low meadows, often along streams, O5 Q2, Avon 1 (Fell, 1957, WIS). (Rol.)

+*A. vulgaris L. Common mugwort. Railroad, Q8.

+ Aster borealis (Torr. & Gray) Provanch. (A. junciformis). *Rush aster*. Edge of sphagnum bog, E1.

A. drummondii Lindl. Drummond's aster. Open woods, O1 (Moran, 1976, BELC), O3 O4.

+ A. firmus Nees (A. lucidulus) *Shining aster*. Wet meadows, R2 S3. This species was included under *A. puniceus* in the Flora.

+ A. firmus × A. simplex (or A. f. × A. borealis). *Aster*. Boggy ground, Avon 23 (*Fell*, 1957, WIS). (Verif.: A. G. Jones, 1980.)

A. ontarionis Wieg. (A. pantotrichus). Ontario aster. Low woods, thickets, D1 T5; frequent.

+ Å. praealtus Poir. (A. coerulescens *sensu* Shinners). *Willow aster*. Low ground, Avon 23, Avon 30 (both *Fell*, 1957, WIS); moist thickets, low meadows, and riverbanks. This material was previously included with *A. simplex*.

A. shortii Lindl. Short's aster. Mesic woods, Magnolia 36 SE, Beloit 28 (Brunsell, 1968, WIS); 4 mi. SE of Orfordville (Anthoney, 1936, WIS).

A. simplex Willd. *Tall white aster*. Var. simplex: Damp open ground, Porter 6 (Wilson, 1964, WIS). Some of our commonest species of aster, especially those (A. simplex, A.

- ontarionis, A. pilosus, and A. tradescantii) typical of low open ground, can be found growing in proximity to one another in many localities in Rock Co., such as along Turtle Creek at Shopiere, the railroad yard at Clinton, and various sites in the Sugar River Bottoms. Several 1957 Fell collections from these sites have been annotated by A. G. Jones as intermediate between A. simplex and A. tradescantii (P5 T5, Turtle 3) or A. ontarionis and A. tradescantii (T5).
- +A. tradescantii L. *Marsh aster*. Wet ground, Avon 12, Avon 29 (both *Fell*, 1957, WIS); wet prairies, sedge meadows, shrub-carrs, ditches, streambanks, and edges of alluvial woods. Jones' studies (1980) have established that the name *A. tradescantii* ought to be applied to much herbarium material (including the specimens cited here) previously identified as *A. interior* [= *A.* × *interior* (Torr. & Gray) Wieg. (*pro sp.*)]. True *A. tradescantii* is infrequent but widespread in Wisconsin.
- A. umbellatus Mill. *Flat-topped aster*. Low prairies, fens. Var. umbellatus: M1 S3 T6. Var. pubens Gray (A. pubentior): O5.
- Cacalia atriplicifolia L. *Pale Indian plantain*. Mesic prairies, G2 M1 P4 Q8; open woods, R1.
- *Carduus nutans L. var. leiophyllus (Petr.) Arenes. *Nodding* or *musk thistle*. Pastures, fields, roadsides, Bradford 19 W, Harmony 31 SE; Hwy. 59 at Badfish Creek; Kellogg Ave., Janesville. This thistle, now a noxious weed in southeastern Wisconsin, has been spreading west and north in recent years (see Tans & Read 1975, pp. 134–135).
- *Centaurea maculosa Lam. *Star thistle, spotted knapweed*. Railroad ballast, Q8, Turtle 29 E. Spreading rapidly in our region.
- +*C. solstitialis L. *Yellow star* or *Barnaby's thistle*. Disturbed hillside, Fulton 7 N (*Stark & Fitzsimmons s.n.*, 1971, WIS). Second Wisconsin collection.
- +*Chrysanthemum balsamita L. Costmary, mint-geranium. Roadside, Union 19 (Eberhart, 1983, WIS).
- Cirsium altissimum (L.) Spreng. *Tall* or *wood thistle*. Low woods, O1 (*Fell*, 1957, WIS). + C. altissimum × C. discolor. *Thistle*. Wooded ravine, H2. (Verif.: G. B. Ownbey,
- 1980.) The specimen originally identified as *C. altissimum* has been placed here on account of the shape and prickliness of leaves and phyllaries.
- +*Crepis tectorum L. Hawk's beard. Railroad ballast, Fulton 5 (Elmhorst, 1978, WIS).
- +*Echinacea purpurea (L.) Moench. *Broad-leaved purple coneflower*. Wooded fencerow, Q2, one plant. Adventive in our area.
- Eupatorium altissimum L. *Tall boneset*. Prairies, Q8 R2; old field, Rock 25 NE. (Rol.) +*Galinsoga parviflora Cav. *Smooth Peruvian daisy*. Driveway, Beloit 36 NE.
- Lactuca canadensis L. White lettuce. Var. canadensis: field, Rock 29 S. Var. latifolia Ktze.: open woods, Lima 30 (Mori, 1965, WIS). Var. longifolia (Michx.) Farw.: open woods, R1.
- Prenanthes racemosa Michx. *Glaucous rattlesnake-root*. Wet- to dry-mesic prairies, G2 P5. (Rol.)
- *Ratibida columnaris (Sims) D. Don (R. columnifera). *Prairie coneflower*. Disturbed dry prairie, Q9 (*Moran*, 1975, BELC). Widely scattered in Wisconsin, where adventive along railroads and in old fields, gravel pits, and waste ground. There is little doubt that this species of the Great Plains prairies is introduced rather than native in the state.
- Rudbeckia triloba L. Brown-eyed Susan. Low open ground, D1 H4 Q2 R1. (Rol.)
- Senecio pauperculus Michx. *Northern ragwort*. Dry sandy or gravelly open woods, prairies, fields, roadsides, sometimes wet fields, ditches, M2 Q1 T5 T6, Plymouth 12 NE, Beloit 31 NE. The L2 and S1 records previously reported as *S. pauperculus*, as well as the L2 record for *S. aureus*, have been referred to *S. semicordatus* by R. R. Kowal.
- S. plattensis Nutt. *Prairie groundsel*. Sandy bank, Avon 21 (*Boebel & Laube*, 1964, WIS); Beloit (*McIlheny*, s.d., WIS); dry sandy or rocky banks, hillsides, and roadsides. Most previous records for S. plattensis in southern Wisconsin, including those reported by us, should apparently be referred to S. pauperculus, the commonest groundsel in Rock Co. and the state as a whole.
- + S. semicordatus Mack. & Bush (S. aureus s., S. pseudaureus s.). *Golden ragwort*. Low prairies, fens, shrub-carrs, L2 S1 T3. Here treated as specifically distinct on the suggestion of R. R. Kowal.

Solidago canadensis L. *Canada goldenrod*. Var. canadensis: railroad, La Prairie 2. Var. hargeri Fern. (S. c. gilvocanescens *sensu* Fern.): fields, meadows, clearings, roadsides, borders of woods, D7 M1 Q1 Q2 T1 T5; very common. Var. scabra Torr. & Gray (S. altissima): prairies, fields, roadsides, fencerows, D7 H2 N1 O5 O7 P3 S3 T6; very common. A treatment published by Croat (1972) applies varietal rather than specific status to the principal taxa of the *S. canadensis* complex.

S. gymnospermoides (Greene) Fern. Goldenrod. Railroad, I2. (Rol.)

Xanthium strumarium L., sensu lato. Weed, especially of old fields, cult. ground, and waste places, D1, Newark 29 N, Newark 31 SE (*Lynch*, 1965, WIS); corner of Prairie and Huebbe, Beloit.

DOUBTFUL AND EXCLUDED SPECIES

Several species for reasons enumerated below must be deleted from the Rock County flora. Users of this flora are invited to submit to the authors collections in support of these

rejected reports and any other novelties they might find.

A. Changes of name as a result of re-identification. A few of our original identifications were in error. Some of the corrected determinations represent species and hybrids not previously reported for the county. They are added to the list (with a "+"). Other changes involve previously reported species and represent either now rejected stations for otherwise accepted species or taxa for which no authentic Rock County specimens are now known. In the latter category are Lycopodium complanatum, Botrychium multifidum, and Gratiola neglecta, which are thus removed from the county flora.

B. Published records lacking voucher specimens. Previously attributed to Rock Co. but not repeated in the present list are Aplectrum hyemale (Case, 1964), Froelichia floridana (Copeland, 1875), Polygonum careyi (Musselman et al., 1971), and Symphoricarpos orbiculatus (Salamun, 1979). We have never found any voucher specimens in support of these reports. C. Subtractions of sight records. The original list includes a few sight records (indicated by "!") communicated to us by people knowledgeable in Wisconsin floristics for which no actual herbarium specimens have been seen. Although their occurrence is not unexpected, the following taxa are necessarily excluded from the list of the county flora: Botrychium dissectum var. dissectum, Sparganium androcladum, Corallorhiza odontorhiza, Comptonia peregrina, Arabi-

dopsis thaliana, A Rhamnus lanceolata, and Asclepias purpurascens.

D. Ornamental plants not known outside of cultivation. Some obvious garden ornamentals were orginally listed because labels on herbarium specimens give no indication that any of them were made from cultivated plants. The prime source of such specimens is the Skavlem Herbarium, now almost all at WIS but with a few collections at MIL. Halvor L. Skavlem (1942–1936) and his sister Gertrude J. Skavlem collected actively during the years of 1889, 1890, and 1915. Their specimens are labeled merely as "Janesville" ("Beloit" or "Harmony" [Twp.] in a few cases), and they are without any data as to habitat or status. Since these collections contain an astonishingly high representation of common cultivated herbs and shrubs, it seems best to exclude many of the records based on them. It is entirely unlikely that such a large array of horticultural introductions should appear as legitimate escapes at essentially the same time and place and be found by the same collectors. Therefore, even though they might have been published in our original paper or other floristic treatments covering the state of Wisconsin, the following species are herewith excluded: Convallaria majalis, Dianthus barbatus, D. plumarius, Clematis recta, Delphinium ajacis, D. × cultorum, Dicentra spectabilis, Papaver rhoeas, Geranium pusillum, Hibiscus moscheutos ssp. palustris, Malva moschata, Eryngium leavenworthii, Syringa persica, Anagallis arvensis, Hyssopus officinalis, Lamium maculatum, Vibur-

⁴The only material purporting to be *Arabidopsis thaliana* from Wisconsin is a single small specimen of *Arabis lyrata* from Dane Co. (*J. Thomson* in 1969, WIS). Since this collection is the basis of the published report in Fassett (1976, p. 182), *A. thaliana* must now be excluded from the flora of Wisconsin.

num opulus cv. roseum, Valeriana officinalis, Anaphalis margaritacea, Chrysanthemum coronarium, and Dahlia pinnata. A few additional records, notably those collected by G. B. Olds, are evidently also horticultural introductions and therefore considered too unreliable to list. These include Dianthus deltoides, Deutzia gracilis, Lycium halimifolium and undoubtedly also others not vet encountered in herbaria.

Other old specimens bearing identical Skavlem or Olds labels represent introduced species which are maintained on the list, either because (1) additional specimens confirm the presence of these species in the county (e.g., Populus × gileadensis, Salix alba, Silene noctiflora, Alcea rosea, Syringa vulgaris); (2) our experience with the flora of the region indicates that they might well have been collected as weeds, escapes, or waifs (e.g., Agrostemma githago, Linum usitatissimum); or (3) such weedy plants are not encountered in the usual horticultural flora (e.g., Bromus commutatus, Arenaria serpyllifolia, Lithospermum arvense).

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REVIEW

FLOWERS OF THE WILD, Ontario and the Great Lakes Region, by Zile Zichmanis and James Hodgins. 1982. Oxford University Press, Toronto. XIV + 272 pp. \$35 CAN (hardcover).

The body of this book consists of a color photograph, full-page line drawing, and brief text for 127 species. The text accompanies the color photo on the right-hand page, and the line drawing is on the left-hand page. The drawings sometime illustrate up to three related species besides the one photographed. The text gives information about habitats, distribution in Ontario, duration, flowering times, culture, notes about similar species, literature for further reading, and sometimes other information. Brief introductory material deals with plant names, explains what information is given in the text for each species, and maps the natural vegetation regions of Ontario. At the end of the text is a glossary, an appendix with Ojibway and French names, a short bibliography, and indices to common and scientific names.

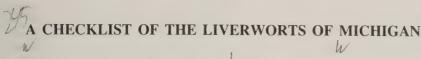
I was unable to find any logic to the selection of species. Photographs and drawings illustrate such uninspiring weeds as *Chenopodium album*, *Plantago major*, and *Xanthium strumarium*. On the other hand, some species treated, such as *Geum triflorum*, are quite rare in Ontario and much of the Great Lakes region. The plants are listed in alphabetical order by common name. Indices to scientific and common names are provided, but if you know a wildflower only by a name other than one used, you will have a hard time finding the plant. The information presented is generally accurate, although the nomenclatural information in the introduction is incorrect. The correct scientific names for plants are not "agreed upon at an international botanical congress." Although the names used are said to be "primarily those used in the New Britton and Brown Illustrated Flora," the authors have not corrected those few names that need updating—*Actaea alba* (correctly *A. pachypoda*), *Lychnis alba* (correctly *Silene pratensis*), *Opuntia compressa* (correctly *O. humifusa*) and *Silene cucubalis* (correctly *S. vulgaris*).

The line drawings are very good and quite attractive. The plate with Allium tricoccum has two additional species illustrated but not named (apparently Allium cernuum on the right and A. canadense on the left). Most of the photographs are good, but some are mediocre and a few bad. Especially poor are those of Allium tricoccum, Oxalis montana, and Podophyllum peltatum. The color rendition of some blues and pinks is inaccurate, most noticeably in the photo of Campanula rotundifolia. Two photographs are misidentified. That of Sisyrinchium montanum is S. mucronatum with wiry, narrow stems and purplish spathes, and that of Utricularia vulgaris is certainly U. cornuta growing terrestrially in a marl flat.

In some respects, this book suffers from being undecided as to whether it is a reference book or a decorative coffee table volume. If the former, the drawings and photographs could have been cropped and placed on the same page, with the text beneath. This would have produced a more compact and inexpensive volume. If the latter, some of the poorer photo-

graphs should have been replaced.

While the dust jacket's claim that this book "will amaze both flower lovers and professional and amateur botanists" may not be fully realized, this is a pleasant and attractive book. It lacks a clear theme but does present useful and generally accurate information. At \$35.00 CAN, it is somewhat expensive, especially if it is to be used as a reference book. But, criticism aside, it is a better quality production than most illustrated wildflower books, although limited in coverage to 127 species.—A. A. Reznicek



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This checklist attempts to bring up to date the many changes and additions to the liverwort flora of Michigan since Steere's publication of a list of 132 species in 1947. The present list of 161 species, arranged in alphabetical order, provides a single reference citation for each species and follows the nomenclature of Stotler & Crandall-Stotler (1977). A list of synonyms is provided. The omission of all taxa below the rank of species is a deliberate action because of different species concepts by different authors. Species which are doubtfully part of the flora, though often cited, and those with a single published report, are indicated by an asterisk.

Anastrophyllum helleranum (Nees) Schust.⁷

A. minutum (Schreb.) Schust. 17

*A. saxicola (Schreb.) Schust. 13

A. michauxii (Web.) Buch¹⁷

Aneura pinguis (L.) Dum.²

Anthelia juratzkana (Limpr.) Trev. 12

Anthoceros macounii M.A. Howe²⁰

Asterella gracilis (Web.) Underw. 12

*Barbilophozia atlantica (Kaal.) K. Müll. 1

B. attenuata (Mart.) Loeske¹⁷

B. barbata (Schmid.) Loeske⁷

B. hatcheri (Evans) Loeske1

B. kunzeana (Hüb.) Gams12

B. lycopodioides (Wallr.) Loeske¹⁷

B. quadriloba (Lindb.) Loeske¹⁷

Bazzania trilobata (L.) S. Gray⁷

Blasia pusilla L.22

Blepharostoma trichophyllum (L.) Dum.5

Calypogeja fissa (L.) Raddi⁵

C. integristipula Steph.6

C. muelleriana (Schiffn.) K. Müll. 17

*C. neesiana (Massal. & Carest.) K. Müll. 17

C. sphagnicola (Arn. & Perss.) Warnst. & Loeske²³

C. suecica (Arn. & Perss.) K. Müll. 17

*C. trichomanis (L.) Corda17

Cephalozia bicuspidata (L.) Dum.5

C. catenulata (Hüb.) Lindb.9

C. connivens (Dicks.) Lindb.6

C. lacinulata (Jack) Spruce¹⁸

C. leucantha Spruce¹³

C. loitlesbergeri Schiffn. 18

C. lunulifolia (Dum.) Dum.5

C. macounii (Aust.) Aust. 18

C. pleniceps (Aust.) Lindb. 23

Cephaloziella arctica Bryhn & Douin 19

C. divaricata (Sm.) Schiffn. 19

C. elachista (Jack) Schiffn. 19

C. hampeana (Nees) Schiffn. 19

C. rubella (Nees) Warnst. 19

C. spinigera (Lindb.) Schust. 19

Chiloscyphus pallescens (Ehrh.) Dum.5

C. polyanthos (L.) Corda²

Cladopodiella fluitans (Nees) Joerg.23

Cololejeunea biddlecomiae (Aust.) Evans⁷

Conocephalum conicum (L.) Lindb.5

Cryptocolea imbricata Schust. 10

Diplophyllum apiculatum (Evans) Steph.5

Fossombronia cristula Aust. 10

F. foveolata Lindb.20

Frullania bolanderi Aust.7

F. brittoniae Evans⁷

F. eboracensis Gottsche⁵

F. inflata Gottsche12

F. oakesiana Aust.6

*F. plana Sull.3

F. selwyniana Pears.³

F. tamarisci (L.) Dum.20

Geocalyx graveolens (Schrad.) Nees⁵

Gymnocolea inflata (Huds.) Dum. 15

Harpanthus drummondii (Tayl.) Grolle²

H. scutatus (Web. & Mohr) Spruce¹⁹

Jamesoniella autumnalis (DC.) Steph.5

*Jungermannia confertissima Nees1

J. crenuliformis Aust.5

J. exsertifolia Steph. 17

J. gracillima Sm.

J. hyalina Lyell¹⁷

J. leiantha Grolle⁵

J. polaris Lindb. 13

J. pumila With.5

J. pyriflora Steph. 13

J. sphaerocarpa Hook.²

Kurtzia setacea (Web.) Grolle²³

Lejeunea cavifolia (Ehrh.) Lindb. emend. Buch⁵

Lepidozia reptans (L.) Dum.5

Leucolejeunea clypeata (Schwein.) Evans³

*Lophocolea bidentata (L.) Dum. L. heterophylla (Schrad.) Dum.5

L. minor Nees⁵

Lophozia alpestris (Schleich.) Evans¹⁷

L. ascendens (Warnst.) Schust. 17

L. badensis (Gottsche) Schiffn.²

L. bicrenata (Schmid.) Dum.

L. capitata (Hook.) Macoun⁵

L. collaris (Nees) Dum.

L. excisa (Dicks.) Dum.⁵

L. gillmanii (Aust.) Schust.²

*L. grandiretis (Lindb.) Schiffn. 12

L. groenlandica (Nees) Macoun¹⁷

L. guttulata (Lindb. & Arn.) Evans⁷ L. heterocolpa (Thed.) M.A. Howe⁷

L. incisa (Schrad.) Dum.⁵

*L. latifolia Schust. 11

L. laxa (Lindb.) Grolle¹⁷

L. longidens (Lindb.) Macoun²

L. obtusa (Lindb.) Evans¹⁷

L. rutheana (Limpr.) M.A. Howe¹⁷

L. ventricosa (Dicks.) Dum.²

Mannia sibirica (K. Müll.) Frye & Clark⁸

M. triandra (Scop.) Grolle¹² Marchantia polymorpha L.5

Marsupella emarginata (Ehrh.) Dum. 18

M. paroica Schust. 12

M. sparsifolia (Lindb.) Dum. 18

M. sphacelata (Gies.) Dum. 10

Metzgeria conjugata Lindb.20

M. furcata (L.) Dum.6

Moerckia hibernica (Hook.) Gottsche²⁰

Mylia anomala (Hook.) S. Gray²³

Notothylas orbicularis (Schwein.) Sull.20

Nowellia curvifolia (Dicks.) Mitt.

Odontoschisma denudatum (Mart.) Dum. 18

O. elongatum (Lindb.) Evans¹⁸

O. macounii (Aust.) Underw. 18

Pallavicinia lyellii (Hook.) Carruth. 10

*Pedinophyllum interruptum (Nees) Kaal. 1

Pellia endiviifolia (Dicks.) Dum. 20

P. epiphylla (L.) Corda⁵

P. neesiana (Gottsche) Limpr.⁵

Phaeoceros laevis (L.) Prosk.5

Plagiochila porelloides (Torrey) Lindenb.⁵

Porella pinnata L.²

P. platyphylla (L.) Pfeiff.⁷

P. platyphylloidea (Schwein.) Lindb.²

Preissia quadrata (Scop.) Nees

Ptilidium ciliare (L.) Hampe⁵

P. pulcherrimum (Web.) Hampe⁵

Radula complanata (L.) Dum.

R. obconica Sull. 19

Reboulia hemisphaerica (L.) Raddi⁵

Riccardia latifrons Lindb.5

R. multifida (L.) S. Gray⁷

R. palmata (Hedw.) Carruth.⁷

*Riccia beyrichiana Hoffm.4

*R. bifurca Hoffm.4

*R. canaliculata Hoffm.4

*R. cavernosa Hoffm.4

R. fluitans L.20

*R. hirta (Aust.) Underw.⁴

*R. sullivantii Aust.4

Ricciocarpus natans (L.) Corda²⁰

Scapania apiculata Spruce¹⁸

S. curta (Mart.) Dum. 18

S. cuspiduligera (Nees) K. Müll. 18

S. glaucocephala (Tayl.) Aust. 18

S. gymnostomophila Kaal. 18

S. irrigua (Nees) Gottsche¹⁸

S. ligulata Buch¹⁸

S. mucronata Buch 18

S. nemorosa (L.) Dum.⁵

S. paludicola Loeske & K. Müll. 18

S. paludosa (K. Müll.) K. Müll.²⁰

S. saxicola Schust.8

S. subalpina (Nees) Dum. 18

S. undulata (L.) Dum. 18

Trichocolea tomentella (Ehrh.) Dum. 16

Tritomaria exsecta (Schmid.) Loeske²

T. exsectiformis (Breidl.) Loeske⁸ *T. heterophylla Schust. 14

T. quinquedentata (Huds.) Buch¹²

T. scitula (Tayl.) Joerg.8

SYNONYMS

Anthoceros laevis L. = Phaeoceros laevis

Asterella ludwigii (Schwaegr.) Underw. = A. gracilis

Calypogeia = Calypogeja

C. meylanii Buch = Calypogeja integristipula

C. paludosa Warnst. = Calypogeja sphagnicola

Cephalozia compacta Warnst. = C. connivens

C. media Lindb. = C. lunulifolia

Cephaloziella byssacea (Roth) Warnst. = C. divaricata

C. myriantha (Lindb.) Schiffn. = C. rubella

C. sullivantii (Aust.) Evans = C. rubella

Chiloscyphus fragilis (Roth.) Schiffn. = C. pallescens

C. rivularis (Schrad.) Loeske = C. polyanthos

Diplophyllum gymnostomophilum (Kaal.) Kaal. = Scapania gymnostomophila

Frullania asagrayana Mont. = F. tamarisci

Grimaldia rupestris Lindb. = Mannia triandra

Isopaches bicrenatus (Schmid.) Buch = Lophozia bicrenata

I. hellerianus (Nees) Buch = Anastrophyllum helleranum

Jungermannia cordifolia Hook. = J. exsertifolia

J. gillmanii Aust. = Lophozia gillmanii

J. lanceolata L. = J. leiantha

J. schiffneri (Loitlesb.) Evans = J. polaris

Leiocolea badensis (Gottsche) Joerg. = Lophozia badensis

L. gilmanii (Aust.) Evans = Lophozia gillmanii

L. heterocolpa (Thed.) Buch = Lophozia heterocolpa

L. obtusa (Lindb.) Buch = Lophozia obtusa

L. rutheana (Limpr.) Evans = Lophozia rutheana

L. schultzii (Schmid.) Buch = Lophozia rutheana

Lepidozia setacea Mitt. = Kurtzia setacea

Lophozia attenuata Dum. = Barbilophozia attenuata

L. barbata Dum. = Barbilophozia barbata

L. hatcheri Evans = Barbilophozia hatcheri

L. inflata Howe = Gymnocolea inflata

L. kaurini (Limpr.) Steph. = L. gillmanii

L. kunzeana (Hübn.) Evans = Barbilophozia kunzeana

L. lycopodioides (Wallr.) Cogn. = Barbilophozia lycopodioides

L. lyoni (Tayl.) Steph. = Tritomaria quinquedentata

L. marchica (Nees) Steph. = L. laxa

L. mildeana (Gottsche) Schiffn. = L. capitata

L. muelleri (Nees) Dum. = L. collaris

L. porphyroleuca (Nees) Schiffn. = L. guttulata

L. quinquedentata (Huds.) Cogn. = Tritomaria quinquedentata

L. schultzii (Nees) Schiffn. = L. rutheana

L. silvicola Buch = L. ventricosa

Mannia rupestris (Nees) Frye & Clark = M. triandra

Marsupella sullivantii (De Not.) Evans = M. sphacelata

Microlepidozia setacea (Web.) Joerg. = Kurtzia setacea

Moerckia flotowiana (Nees) Schiffn. = M. hibernica

Nardia crenuliformis Lindb. = Jungermannia crenuliformis

N. hyalina Carring. = Jungermannia hyalina

Orthocaulis atlanticus (Kaal.) Buch = Barbilophozia atlantica

O. attenuatus (Mart.) Evans = Barbilophozia attenuata

O. gracilis (Schleich.) Buch = Barbilophozia attenuata

O. kunzeanus (Hüb.) Buch = Barbilophozia kunzeana

O. quadrilobus (Lindb.) Buch = Barbilophozia quadriloba

Pellia fabroniana Raddi = P. endiviifolia

Plagiochila asplenioides (L.) Dum. = P. porelloides

Plectocolea crenulata (Smith) Evans = Jungermannia gracillima

P. crenuliformis (Aust.) Mitt. = Jungermannia crenuliformis

P. hyalina (Lyell) Mitt. = Jungermannia hyalina

Preissia commutata Nees = P. quadrata

Riccardia pinguis (L.) S. Gray = Aneura pinguis

Riccia rhenana Lorbeer = R. fluitans

- R. arvensis Aust. = R. bifurca
- R. crystallina L. = R. cavernosa
- Scapania buchii K. Müll. = S. lingulata
- S. dentata Dum. = S. undulata
- S. microphylla Warnst. = S. lingulata
- Scapaniella glaucocephala (Tayl.) Evans = Scapania glaucocephala
- Solenostoma appalachianum Schust. = Jungermannia pyriflora
- S. cordifolia (Hook.) Steph. = Jungermannia exsertifolia
- S. crenuliformis (Aust.) Steph. = Jungermannia crenuliformis
- S. gracillimum (Sm.) Schust. = Jungermannia gracillima
- S. hyalina (Lyell) Mitt. = Jungermannia hyalina
- S. levieri (Steph.) Steph. = Jungermannia confertissima
- S. pumilum (With.) K. Müll. = Jungermannia pumila
- S. pyriflorum Steph. = Jungermannia pyriflora
- S. schiffneri (Loitlesb.) Evans = Jungermannia polaris
- S. sphaerocarpum (Hook.) Steph. = Jungermannia sphaerocarpa
- Sphenolobus exsectiformis Steph. = Tritomaria exsectiformis
- S. exsectus Steph. = Tritomaria exsecta
- S. hellerianus Steph. = Anastrophyllum helleranum
- S. michauxii (Web.) Buch = Anastrophyllum michauxii
- S. minutus (Crantz) Steph. = Anastrophyllum minutum
- S. saxicola (Schrad.) Steph. = Anastrophyllum saxicola

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Notice

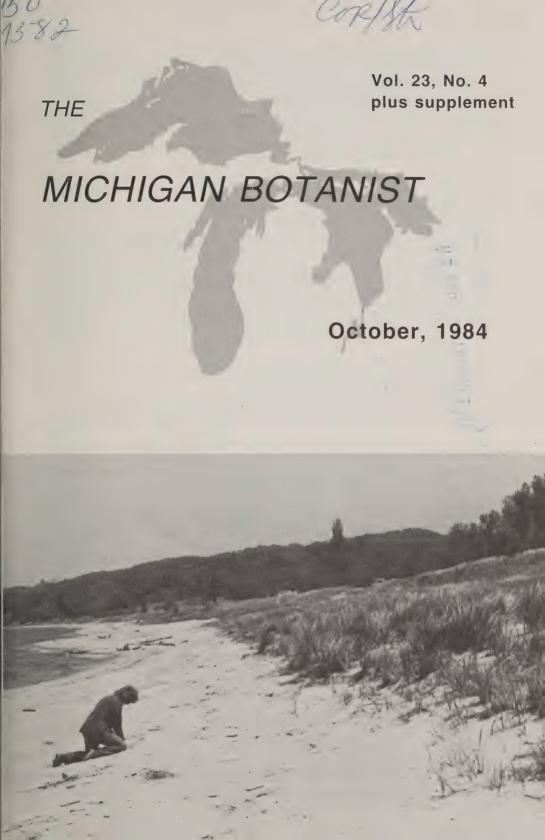
Beginning May 1 of this year, James and Nancy Weber will take over the editorship of *The Michigan Botanist*. I have very much enjoyed serving as editor these many years. I never quite achieved the standard of excellence set by E. G. Voss, nor did I really expect to, but I have been gratified to see that the journal has continued to have a rich and varied composition, owing to a diverse, interesting, and capable authorship. Anton Reznicek has been very useful to me, keeping the journal just barely solvent by some special magic that he has. I am grateful for the help of the editorial board—Burton Barnes, John Beaman, James Pringle, Helen Smith, Edward Voss, and Ellen Weatherbee—for advice and support and also the Board of Directors of the Michigan Botanical Club for many useful suggestions. I also owe thanks to the many persons who cheerfully helped with the review of papers and their basic improvement.

I am pleased to be succeeded by co-editors of unusual competence and bright promise.

HOWARD CRUM

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SPECIES COMPOSITION AND DIVERSITY OF A MESIC PRAIRIE RELICT IN KALAMAZOO COUNTY, MICHIGAN

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About 80,000 acres of mesic prairie existed in Michigan in patches big enough for the pioneers to name (Veatch 1927, Butler 1947–48). These lands were occupied by the earliest settlers (Peters 1970) and through the years have been prime sites for agriculture and development. Mesic prairie is now exceedingly rare in the state; most remaining native grasslands are wet or sand prairie or the remnants of oak savanna (Chapman 1983). Here I describe species composition and diversity patterns in a small relict of Genesee Prairie, a mesic prairie in Kalamazoo County.

STUDY AREA

The remnant was east of Oshtemo (NW½, SE¼, Sec. 25, R 12 W, T2S) at the northern border of the original prairie (Hodler et al. 1981). Like the wet prairie described in Brewer (1965), the Oshtemo prairie was on the right-of-way of the earliest railroad of the region. Construction was about 1847, or 18 years after the first settlers arrived on Genesee Prairie (Butler 1948). Steam-driven trains ran on the line until 1924 when the company then operating it went into receivership (Brock 1955). By 3 July 1929 the rails had been removed and the right-of-way sold to American Telephone and Telegraph. Lines were installed on poles; brush was managed by cutting and, later, by herbicide applications at less-than yearly intervals to the bases of the woody plants. These ceased late in the 1970s with large-scale alteration of the site that included burial of the lines.

The study area consisted of a strip about 190 m long by 15 m wide running east from 11th Street. The abandoned roadbed ran east-west in a cut 4–6 m below the surface of the surrounding land (Fig. 1). The roadbed was 7–8 m wide and the north-facing slope 4.5–5.5 m. The width of the level-ground section (ridgetop) that was studied was the 1.5–4.5 m lying between the crest of the slope and a wheel-track. The south-facing slope of the cut had a large amount of woody vegetation and is not considered in this paper.

Before 1962, similar vegetation occupied an additional 300 m to the east but this portion was destroyed in the construction of U.S. highway 131.

METHODS

Soil samples were taken from the top 8 cm. Determinations of pH in the field was made colorimetrically using LaMotte-Morgan indicators. For soil moisture determinations, cans were sealed with masking tape in the field and

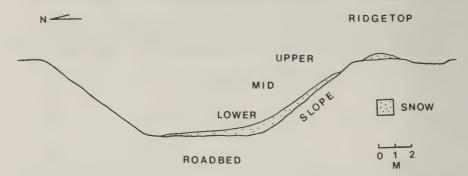


Fig. 1. Profile of Oshtemo Prairie, showing sampling sites. Snow cover is as of 24 March 1967; snow depth is exaggerated slightly.

removed to the laboratory for weighing. After oven-drying at 110°C for 36–48 hours, reweighing allowed expression of soil moisture as a percent of soil dry weight. Soil pH readings were made on 6 dates between June 1962 and November 1963 and also on 23 January 1974. Soil moisture was determined on 5 days, two in July and three in September between 1961 and 1964. Soil texture was determined by feel using the methods in Thien (1979) and Brewer & McCann (1982).

Slope was measured with a clinometer. Soil, surface, and air temperatures on the various sites were measured on eight dates between January 1962 and February 1967 using standard chemical thermometers.

Species composition was determined by list quadrats of 1 m² taken in transects parallel with the long axis of the study area. Separate transects were taken for ridgetop (RT), roadbed (RB), upper third of the slope (US), middle third (MS), and lower third (LS). The slope samples were later combined for most purposes. Intervals between quadrats, determined before each set of transects, varied between two and eight meters. Sampling dates and numbers of quadrats were as follows: Ridgetop—20 quadrats, 7–10 Sept. 1961; 30, 16 July–1 Aug. 1962. Roadbed—12, 10–26 Sept. 1961; 42, 27 June 1962; 18, 14 Aug. 1962. Slope—35, 30 June–13 July 1962; 74, 7 Sept.–5 Oct. 1962. In addition, 20 quadrats were taken on the roadbed, 60 on the slope, and 25 on the ridgetop 3 May 1963 for vernal species poorly sampled previously. Also 40 quadrats were taken on the slope and 40 on the ridgetop on 30 August 1963 to separate a few species that had been confused in earlier sampling.

I wanted to measure two aspects of species diversity: the mean number of species per m² quadrat and the total number of species in an accumulation of quadrats. For comparisons these needed to be from a restricted time period and the same number had to be used for each site. Late summer-early fall 1962 (16 July–27 September) was the most suitable time. The limiting sample size was for the roadbed, where 18 quadrats had been taken during that period. Accordingly, 18 quadrats were selected from the larger number available for each of the other sites by choosing the consecutive quadrats that

occurred in the same section of the study area (approximately the middle two-fifths).

Plant names follow Gleason & Conquist (1963) and Courtenay & Zimmerman (1972).

RESULTS

The original soil survey of the county (Perkins & Tyson 1928) mapped the study area as a small southward projection of Fox silt loam into a large area of Warsaw silt loam. Warsaw loam was the name then given to soils on which most of the historic prairies of the county occurred; Fox silt loams were said to be "forested, but it appears in places that the change from a prairie condition to forest has taken place in comparatively recent times, inasmuch as the resemblance to the Warsaw profile is marked." Some correlation between bur oak openings (as mapped in Hodler et al. 1981) and the Fox series seems to exist. The current soil survey (Austin 1979) maps the site as "Urban land—Kalamazoo Complex" (which cannot be denied) and has it adjacent to either Kalamazoo loam or Dowagiac loam.

My own determinations of the ridgetop and slope soils indicated a sandy clay loam structure. In both locations the topsoil was dark from organic matter but the depth and darkness was greater on the ridgetop. It seems possible that the ridgetop may have represented original prairie soil, although the surface was certainly disturbed during the construction of the railroad. The slopes, however, must have been new surfaces on which succession began about 1847.

Succession presumably began on the roadbed between 1924 and 1929 when the rails, but not the ballast or ties (many of which were still discernible during my sampling) were removed. The soil of the roadbed consisted of ballast plus smaller particles resulting from weathering and erosion. There was little evidence of current erosion from the slopes despite their steepness (about 37°).

The roadbed was clearly the driest site (Table 1), owing probably to its coarse texture. Contrary to my expectations there was no catena-like trend from dry soil at the ridgetop to wet at the lower slope. Rather, the rank among the ridgetop and slope sites shifted from date to date. Considering both soil moisture and protection from wind, the lower slope was slightly more hydric than the other sites, which are indistinguishable from one another.

The roadbed was slightly alkaline (Table 1); some (but not the majority) of the gravelly material remaining from the ballast was limestone. The median pH of the lower slope was also above neutral but less alkaline than the roadbed. The other locations were slightly to moderately acid. Readings overlapped but the midslope tended to be least, and the upper slope most, acid.

Certain microclimatic differences would be expected among the various sites based on the flatness of the roadbed and ridgetop and the northern

TABLE 1. Soil moisture and pH at Oshtemo Prairie by site.

	Location				
Trait	RT	UP	MS	LS	RB
Soil moisture (%)*					
July range	7.5-13.1	6.7-8.7	6.7-17.0	7.2-12.2	1.5-3.7
Sept. range	9.8-31.2	15.2-39.0	13.2-22.6	17.3-35.9	9.0-16.9
Soil pH, upper 8 cm	n = 22	n = 13	n = 15	n = 14	n = 10
Median	6.6	6.0	6.8	7.2	7.8
Range	5.4-6.8	5.0-6.8	5.2-7.8	6.0-7.4	7.0-8.2

^{*}n = 4 except for lower slope-July and middle slope-September where n = 3.

exposure of the slope, along with the location of the roadbed in a steep-sided valley. In a large number of measurements of air, surface, and soil temperatures, these expectations were sometimes fulfilled, but frequently only inconsequential differences were seen among the sites. In some years, snow cover was complete through most of the winter, but in others thaws exposed part or all of the area. In times of partial snow cover the pattern was variable but tended toward that shown in Fig. 1, sketched in early spring after about three months of snow cover. Probably, then, the crest of the hill, including the uppermost slope and the outer portion of the ridgetop, would tend to suffer the greatest temperature extremes during winters of variable snow cover.

FLORISTIC COMPOSITION

Slightly fewer than 100 species were identified (Tables 2,3), mostly in connection with quantitative sampling. No attempt was made to compile a complete flora, and other (infrequent) species were present, possibly including prairie species. About 20 of the recorded species are non native (Tables 2 and 3). They were spread throughout the area, about a dozen occurring on each site; only on the roadbed, however, did they make up an important part of the vegetation (Table 2).

Composites and grasses were the leading families, as is generally true of prairies (e.g., Thompson 1983). Big bluestem (Andropogon gerardii) was the dominant plant species, occurring in three-fourths or more of the quadrats throughout the study area (Table 1). Little bluestem (A. scoparius) was in slightly less than a third of the quadrats on all sites. A few other species were relatively common throughout: bracken fern (Pteridium aquilinum), Canada bluegrass (Poa compressa), flowering spurge (Euphorbia corollata), Indian hemp (Apocynum cannabinum), and spiderwort (Tradescantia ohiensis) are examples.

There were clear differences in species composition among the various sites. Species that were more frequent on the ridgetop than elsewhere were smooth brome (*Bromus inermis*), bastard toadflax (*Comandra umbellata*),

TABLE 2. Percent frequency in m^2 quadrats at Oshtemo Prairie (all species of at least 10% frequency on one site). Species of foreign origin are shown in boldface.

	Site			
Species	Roadbed	Slope	Ridgetop	
Achillea millefolium	0	33.9	2.0	
Agrostis stolonifera	100.0*	25.0*	24.0*	
Agropyron trachycaulum	0	11.9	0	
Andropogon gerardii	93.8	74.3	76.0	
A. scoparius	30.8	31.2	30.0	
Anemone quinquefolia	1.4	13.3	4.0*	
A. virginiana	5.6	32.1	0	
Antennaria plantaginifolia	0	46.8	22.0	
Apocynum androsaemifolium	14.0	12.8	12.0	
Arenaria stricta	30.0*	1.7	0	
Aster laevis	0	19.3	4.0	
A. sagittifolius	1.4	50.5	6.0	
Bromus inermis	0	33.0+	50.0**	
Carex pensylvanica	0	95.0*	84.0*	
Comandra umbellata	0*	0*	24.0*	
Daucus carota	1.4	40.4	24.0	
Draba reptans	10.0*	0	0	
Erigeron strigosus	37.8	0.9	2.0	
Euphorbia corollata	53.2	55.0	54.0	
Fragaria virginiana	1.4	10.1	0	
Galium boreale	2.8	58.3*	24.0*	
Geranium maculatum	0*	28.3*	4.0*	
	5.6	14.7	6.0	
Lactuca canadensis	0	11.9	28.0	
Lathyrus venosa	0	1.8	16.0	
Liatris novae-angliae	53.2	7.3	0	
Melilotus alba	42.0	33.9	2.0	
Monarda fistulosa	5.0*	16.7*	0	
Phlox pilosa	50.0*	30.0*	64.0*	
Poa compressa			04.0	
Potentilla recta	36.4	33.0	22.0	
Pteridium aquilinum	11.2		0	
Ranunculus fascicularis	20.0	3.3		
Ratibida pinnata	42.0	0	6.0	
Rudbeckia hirta	0	14.7	2.0	
Smilacina racemosa	0	10.1	18.0	
Solidago juncea	0	22.5+	25.0**	
S. rigida	4.2	5.5	28.0	
Sorghastrum nutans	1.4	11.0	16.0	
Taenidia integerrima	1.4	15.6	0	
Thalictrum dioicum	0	16.6	0	
Tradescantia ohiensis	18.2	29.4	16.0	
Tragopogon dubius	23.8	2.7	0	
Veronica arvensis	10.0*	0*	0*	
Veronicastrum virginicum	0	11.0	4.0	
Vicia americana	0	15.6	10.0	
Viola sororia	0	10.1	0	

^{*}Based on 3 May 1963 samples

⁺ Upper slope only, 30 Aug. 1963

^{**30} Aug. 1963

TABLE 3. Species recorded at Oshtemo Prairie at frequencies below 10%. Species of foreign origin are shown in boldface.

Ambrosia artemisiifolia RB, RT Angelica venenosa S Asclepias tuberosa RB, S, RT **Asparagus officinalis** S Asplenium platyneuron S Aster pilosus RB, S, RT

Botrychium dissectum S B. matricariaefolium RB

Cicuta maculata S Cirsium sp. S, RT Coreopsis tripteris S

Dactylis glomerata RB, RT Desmodium canadense S, RT Dioscorea villosa S, RT

Elymus candensis RB

Helianthus decapetalus S Hepatica americana S Heuchera richardsonii S Hieracium sp. RB, S, RT Hypericum perforatum RB, S, RT

Lepidium campestre RB, RT Liatris aspera RB, S, RT Lysimachia quadrifolia S Oxalis sp. S, RT

Panicum capillare RB, RT
P. leibergii RT
Phleum pratense RT
Physalis sp. S, RT
Plantago lanceolata S
Poa pratensis RB, S, RT
Podophylum peltatum RT
Polygonatum commutatum S, RT
Potentilla arguta RB
Potentilla simplex RB, S
Prenanthes alba S
Prunella vulgaris S

Rumex acetosella S. RT

Saponaria officinalis RB Smilax herbacea S, RT Solidago canadensis S, RT S. gigantea S S. graminifolia S, RT S. nemoralis RT Sonchus sp. RT Sporobolus cryptandrus RB

Trifolium pratense S, RT

Verbascum thapsus RB, S

New England blazing star (*Liatris novae-angliae*), early goldenrod (*Solidago juncea*), and rigid goldenrod (*S. rigida*).

More than a dozen species were more abundant on the slope than either ridgetop or roadbed. Included were several closely associated with prairie such as yellow pimpernel (*Taenidia intergerrima*), downy phlox (*Phlox pilosa*), Culver's root (*Veronicastrum virginicum*), northern bedstraw, and smooth and arrow asters (*Aster laevis* and *A. sagittifolius*). Also included, however, were several species of wide habitat occurrence such as wood anemone (*Anemone quinquefolia*), wild geranium (*Geranium maculatum*), Queen Anne's lace (*Daucus carota*), woolly blue violet (*Viola sororia*), and yarrow (*Achillea millefolium*).

A few species showed definite trends in frequency within the slope. Wild bergamot (*Monarda fistulosa*) was at least as frequent on the lower slope (49.5%) as on the roadbed (Table 2), but declined to 30.8% at midslope and to 2.3% on the upper slope. Wild geranium, though absent from the roadbed, showed a similar trend within the slope, dropping from 45% on the lower slope to 5% on the upper (similar to the ridgetop, Table 2). Yarrow showed an opposite trend; rare on both ridgetop and roadbed, it was about twice as frequent on mid and upper slopes as on the lower slope.

¹RB—roadbed, S—slope, RT—ridgetop

TABLE 4. Percent frequency by site of all woody plants recorded in m² quadrats at Oshtemo Prairie.

Species	Roadbed	Slope	Ridgetop
Acer sp.	0	0.9	0
Ceanothus americana	0	11.3	12.0
Cornus racemosa	1.4	12.8	12.0
Crataegus sp.	0	0.9	0
Corylus americana	0	11.0	2.0
Populus deltoides	0	7.3	10.0
Prunus serotina	0	2.8	2.0
Quercus velutina	0	3.7	0
Rhus glabra	0	14.9	0
Rhus typhina	12.6	0	0
Rosa carolina	2.8	37.6	18.0
Rubus spp.	0	13.8	32.0
Salix humilis	0	15.6	14.0
Symphoricarpos orbiculatus	0	2.8	0

Several species of high frequency were virtually absent from ridgetop and slope. Some of these were non-native species, such as white sweet clover (Melilotus alba), daisy fleabane (Erigeron strigosus), and meadow goat's beard (Tragopogon dubius); however, coneflower (Ratibida pinnata), a native prairie species, was also much more prominent on the roadbed than elsewhere. The roadbed was also distinctive in totally lacking several frequent species of the slopes and ridgetop; examples are Penn sedge (Carex pensylvanica), Solomon's seal (Polygonatum commutatum), vetch (Vicia sativa), vetchling (Lathyrus venosus), and pussy toes (Antennaria plantaginifolia). Most of the characteristic prairie plants occurring on the roadbed are near-ubiquitous in Michigan prairies (Thompson 1983); exceptions are Arenaria stricta and Draba reptans which are dry prairie species (Betz 1965) and Ranunculus fascicularis which Curtis (1959) considered an oak-opening species.

Thirteen species of woody plants plus two or more species of *Rubus* occurred in my quadrats (Table 4). They were scarcest on the roadbed, where only three species occurred. Included were several shrubby species that are probably characteristic prairie species but there were also woody invaders including cottonwood (*Populus deltoides*), black oak (*Quercus velutina*) and wild black cherry (*Prunus serotina*). No bur oak (*Quercus macrocarpa*) were encountered in the sampling but some were present, including one 12.6 m tall (on 22 Jan. 1974) just south of the wheeltrack on the ridgetop.

DIVERSITY

The slope was significantly ($\alpha=0.05$) more diverse than other sites, having an average of 9–11 species per m² and 45–53 species total (per 18 m²) (Table 5). Comparing mean number of species per m² for the least diverse

TABLE 5. Diversity (number of species) at Oshtemo Prairie by site.

	Per m ²				
Site	Mean	Range	SD	Total, 18 m ²	
Roadbed	6.1	4–9	1.32	20	
Slope					
Lower	9.6	6–15	2.57	45	
Middle	10.7	5-18	3.80	53	
Upper	9.3	4-14	2.80	49	
Ridgetop	6.9	4-14	2.41	34	

slope site (upper slope) with the ridgetop and the roadbed gives t values of 2.13 and 3.29 (df = 34 in each case). Mean number of species per m² on the roadbed was lower than for the ridgetop but not significantly so; however, the roadbed had only 20 total species compared with 34 for the ridgetop.

DISCUSSION

The species list for the ridgetop and slope (Tables 2 and 3) contains 17 of Curtis's (1959) 50 indicator species, distributed as follows: 2 wet prairie, 8 wet-mesic, 5 mesic, 0 dry-mesic, 2 dry. The roadbed held only 9 of the indicator species distributed as 4 wet-mesic, 2 mesic, 1 dry-mesic, and 2 dry. Although Curtis's list of indicators needs modification, especially for Michigan applications, the generally mesic to wet-mesic nature of the slopes and ridgetop and the drier affinities of the roadbed are evident.

The presence of rock sandwort (*Arenaria stricta*) and *Draba reptans*, two characteristic dry prairie species that are uncommon in Kalamazoo County (Hanes & Hanes 1947), on this man-produced dry prairie poses a difficult question: Were they present in the driest parts of Genesee Prairie or did they invade from some greater distance, perhaps along the railroad?

A few other species showed differences in distribution that seem obviously linked to certain environmental features. For example, white sweet clover and sheep sorrel (*Rumex acetosella*) showed expected, opposite, trends based on soil pH. Several weeds seemed most frequent on the sites of greatest soil disturbance (e.g., annual ragweed, *Ambrosia artemisiifolia*, and pepper grass, *Lepidium campestre*). But the sites differed by so many factors (soil pH, moisture, and texture; microclimate; frequency of disturbance; time available for succession) that detailed speculation on the causes of differences in distribution of species by site seems futile.

Curtis (1959) noted that wet-mesic prairies tend to have several species that are otherwise considered forest plants. Among such species at Oshtemo are false Solomon's seal (Smilacina racemosa), wood anemone, wild geranium (Geranium maculatum), grape fern (Botrychium dissectum), hepatica (Hepatica americana), Solomon's seal, lion's foot (Prenanthes alba), carrion flower (Smilax herbacea), and tall meadow rue (Thalictrum dioicum). There are two general sorts of explanation for this phenomenon. Curtis

(1959) suggested that true prairies (as distinguished from brush prairies) resulted from the catastrophic (fire) destruction of mesic forest. These herbs might, then, be relicts of a time when the area was occupied by mesic forest.

The other explanation is a non-historical one, that the combination of physical factors in mesic prairie and in mesic forest are operationally enough alike that both habitats meet the requirements of these species (Curtis 1959). In a sense, this has to be true for the relict hypothesis also but one can envisage situations where relict species could persist but not invade and also situations in which relicts slowly dwindle. Because most of these species occurred on the slope and some even on the roadbed, neither of which ever supported forest, the relict hypothesis seems unnecessary.

The establishment of mesic prairie on the slope by succession beginning about 1847 and its maintenance into the 1970s is noteworthy. Probably fires during the railroad days and, later, brush cutting and herbicide treatments encouraged this community. The development of vegetation allied to xeric prairie on the roadbed by succession beginning 1924–9 is probably related to the brush control plus the relatively extreme nature of the substrate, which must have discouraged some potentially competitive species.

On 23 January 1974 about 10 years after the period of intensive study, the study area was still intact but I noted that there seemed to be much less prairie vegetation and more woody and non-prairie. In the late 1970s commercial development virtually obliterated the study area. The ridgetop was cut down and the valley filled in. Only a few meters next to 11th Street retained the earlier topography. On this remaining section, the ridgetop and slope had become heavily grown up with large-tooth aspen (*Populus grandidentata*) 0.5–18.3 cm dbh (1983 observations).

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SUMMARY

A small remnant of Genesee Prairie lying on the right-of-way of the earliest railroad through Kalamazoo County, Michigan, was studied. Most of it was occupied by mesic prairie. The former roadbed, lying in a 6-m-deep cut and having a substrate derived from ballast, supported vegetation that, in addition to several prairie species of wide amplitude, included some xeric prairie species and several non-native species at high frequencies. The roadbed had the lowest species diversity and the slope to it, the highest. Succession would have begun on the slope following railroad construction in the middle of the 19th century and on the roadbed following cessation of traffic and removal of the rails in the late 1920s. The reestablishment of mesic prairie on the slope was probably encouraged by fires from trains and, later, brush control. The development of a kind of xeric prairie on the roadbed was probably favored by brush control and perhaps also by the relatively extreme soil conditions. Like other wet-mesic prairies (Curtis 1959), the remnant supported several species that otherwise occur primarily in forest.

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PRESETTLEMENT VEGETATION OF SOUTHWESTERN MICHIGAN

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In review of the importance of current land use data sets and land use mapping for environmental planning and the design of ecological research, a need exists for accurate large-scale maps of the original landscape. Although general maps of the presettlement vegetation of the entire state of Michigan have been produced (Marschner 1946, Veatch 1959, Küchler 1964), these maps have lacked detail and accuracy. Consequently, the state is without an adequate map which depicts vegetation distribution as it occurred just prior to white settlement. Although the map supplement accompanying this issue of the *Michigan Botanist* covers only ten counties in southwestern Michigan, it represents a significant step toward fulfilling that need.

This product represents the vegetation of southwestern Michigan as of the years 1825-1832, just prior to significant settlement. It is based on the note of the original land surveys. These surveys, a part of the U.S. Public Land Survey begun in 1785, are a rich source of information on the primeval vegetation of large parts of the United States. Among the earliest published regional maps using such data is one of the Kalamazoo County prepared by Kenover in 1929 (and published in 1930). Kenover (1934, 1940, 1943) later mapped nine other counties in southwestern Michigan in the same way. Kenover's research recognized only six plant associations in southwestern Michigan: beech-maple forests, oak-hickory forests, swamp forests, oakpine forests, bur oak forests, and prairies. Witness trees of hemlock, and white pine outside the oak-pine forest, were also plotted on Kenoyer's maps, although he did not attempt to delineate any additional northern forest types. Brewer (n.d.) created a black and white composite map (Fig. 1) which was compiled from Kenoyer's ten individual county maps plus Livingston's (1903) map of Kent County. (Livingston's map was not based on original land survey data but rather his own observations as of 1900.) The present map supplement includes Eaton County but excludes Ottawa and Kent Counties, and thus represents some locational differences from these earlier studies.

It seemed desirable to re-map the original vegetation within the area for several reasons. A large-scale map produced in color by modern cartographic

production techniques would enhance and expand the ability to depict more vegetation types. Also, it seemed feasible to produce a map that would improve upon Kenoyer's pioneer effort. The organization of the vegetation of the midwestern United States is now better understood, and, with the larger scale, it has been possible to utilize a more precise classification system. The present map depicts twenty-two different vegetation associations identified within the study area: two categories of low density woodland (bur oak opening and oak savanna), five upland forest types, nine swamp or floodplain forests plus five additional wetland classifications, and prairies.

The detailed field survey of the counties' townships and sections took place from 1825 through 1832, shortly after the first white settlers arrived in southwestern Michigan. Information from the original surveyors' notes was entered to scale on U.S. Geological Survey topographic maps, both 7½ and 15 Minute Series Quadrangles. Two kinds of data were used: (1) surveyors' comments on entering and leaving certain vegetation types and (2) information on individual trees, including two witness trees at each section corner, two additional bearing trees at the halfway mark or half section post along each section line, line trees (trees situated directly on section lines although not at critical reference points), and two trees at the point where the section line entered and left a stream or lake. For the area included on this map approximately 55,000 individual trees were recorded. Species, diameter, and distance from the line were recorded in the survey notes for each tree. This information usually allowed vegetational boundaries to be located to within $\pm \frac{1}{4}$ mile or less, depending upon how informative the line trees or the surveyors' additional notes were. Away from the section lines, accuracy was increased by interpretation of contour lines and other information from the topographic maps.

A comparison between Kenoyer's map composite (Fig. 1) and the newer multicolor version reveals several significant differences reliant upon our much refined classification system. First, we were able to classify oak savanna and oak forest vegetation where Kenoyer only utilized an oak-hickory scheme. An example of this can be seen in Branch County were Kenoyer identifies approximately forty percent of the county as oak-oak hickory whereas we found that the majority of that same area lies in the oak savanna classification with some oak forest intermixed. A similar example lies in St. Joseph County where Kenoyer found approximately eighty percent of that county to contain oak-oak hickory forest while we could identify the same area to contain a nearly even split between oak savanna and oak forest.

Second, our ability to refine the wetland classification from a single category in Kenoyer's map to eight swamp forest categories as well as five additional wetland categories greatly improves upon the display of the presettlement vegetation. Particularly lacking in Kenoyer's representation are the categories of marsh and wet prairie (see map supplement for vegetative types of the surveyors included in these two categories). By separating these two categories it was possible to show that the marshes and wet prairies were located almost exclusively in the oak forest and oak savanna whereas the southern swamp forests were found predominantly in the beech-maple for-

VEGETATION OF SOUTHWESTERN MICHIGAN

AT THE TIME OF SETTLEMENT

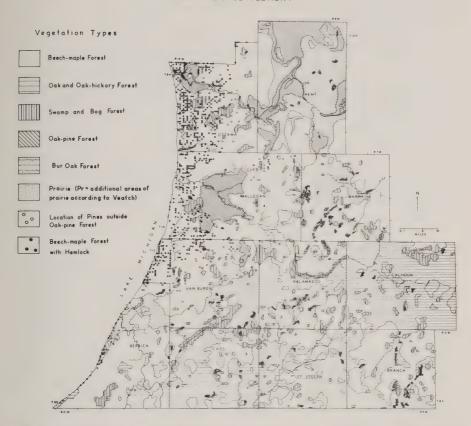


Fig. 1. Compilation of maps by Kenoyer and Livingston of the vegetation of southwestern Michigan at the time of settlement (Brewer, N.D.). Based on Kenoyer (1934, 1940, 1943), Livingston (1903), and Veatch (1959).

ests. The distributional pattern presumably resulted from fire in the oak areas.

Third, we have displayed accurately the location of the forty-nine different prairies within the ten county area. Perhaps one of the major drawbacks to Kenoyer's effort is his mis-identification of prairies. For example in St. Joseph County, Kenoyer depicts several prairies that were clearly identifiable as bur oak openings. Also, in Branch County, where Kenoyer did not distinguish any prairies, we were able to delineate seven prairies (four from original land survey notes and three from historical writings).

Perhaps the greatest advantage of this modern rendition of the presettlement vegetation is the detailed classification scheme utilized in order to delineate the vegetation boundaries. As our abilities to classify increase, our

abilities to display multiply. Therefore, such refinements in classification, along with modern cartographic techniques, allow for this detailed presentation of the presettlement vegetation in the ten counties of southwestern Michigan.

ACKNOWLEDGMENTS

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MAP AVAILABILITY

Additional copies of this map supplement and the Presettlement Vegetation Map of Kalamazoo County, Michigan (Hodler, et al., 1981) are available from: "Vegetation Map", Department of Geography, Western Michigan University, Kalamazoo, MI 49008. Price: \$3.50 plus postage.

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NOTE

As a result of a production error, the first paragraph of the narrative provided on the map supplement should be disregarded. Also, the phrase "silt-loam or mollisol" in the 18th line of the 7th paragraph of the 2nd column on the back of the map should be "loamy mollisol."

FOSSOMBRONIA IN MICHIGAN

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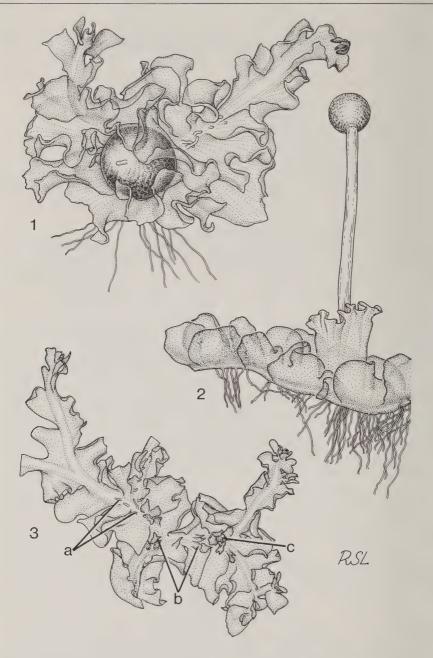
Herbarium, University of Michigan Ann Arbor 48109–1057

The liverwort genus *Fossombronia* is by no means common in the Upper Great Lakes region, and it is therefore gratifying to report two species from the vicinity of the University of Michigan Biological Station in Cheboygan County, Michigan.

Sterile examples of *Fossombronia* have been observed at least three times during the past 30 years at Vincent Lake where plants of this genus appear to have been first discovered by W. R. Tulecke on 12 July 1951 based on a specimen in the herbarium of the University of Michigan Biological Station. Recent collections with spores and elaters make it possible to identify both *F. cristula* Aust. and *F. foveolata* Lindb. from Vincent Lake and, in fact, from the same restricted part of the wet, sandy lake shore. *Fossombronia foveolata* has also been found recently in Cheboygan County at Duck Marsh, near Lake 16, some 20 miles east of Vincent Lake.

In his Liverworts of Southern Michigan, Steere (1940) mentioned an occurrence of Fossombronia cristula at Three Mile Lake, at Paw Paw, Kalamazoo County. (We have not located the voucher specimen for this collection.) Fossombronia cristula has been found on the east side of Lake Huron at Parry Sound, Ontario (C. O. Grassl 7026, MICH). In the northern part of Michigan's Lower Peninsula F. foveolata, new to Cheboygan County, has also been collected once in nearby Presque Isle County, and in the Upper Peninsula it is known from Alger, Marquette (or possibly Baraga), and Ontonagon Counties. Elsewhere in the Lake Superior region it has been collected in Cook County, Minnesota, and several localities in the vicinity of Thunder Bay, Ontario. It has also been found in southern Ontario, in Kent County (W. Stewart, MICH). Schuster (1953), in his Boreal Hepaticae, mentioned two other localities in Minnesota (Anoka and Pine Counties) and cited specimens from Keweenaw and Baraga Counties in northern Michigan. The Baraga County specimen (from Deer Lake) appears to be the same one labeled Marquette County in the Herbarium of the University of Michigan.

Fossombronia cristula (figs. 1, 4, 5–9, 10–13) has reticulate spores and stout, irregular, sometimes branched elaters with a poor development af annular thickenings. In the Vincent Lake collection some few elaters showed loose, imperfect spirals, but most elaters had well-spaced annular thickenings. In contrast F. foveolata (figs. 2, 14–15) has long, slender elaters with tightly bispiral thickenings. The spores of both species (cf. figs. 14–15 and 10–13) are similar. The outer spore faces are strongly and regularly reticulate, while the proximal spore surfaces have an irregular reticulum in which



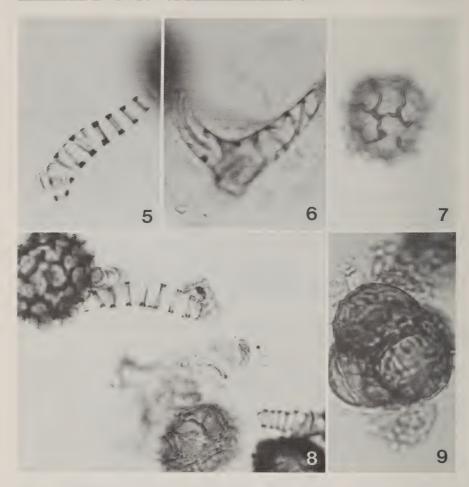
Figs. 1–3. Fossombronia from Vincent Lake, Cheboygan County, Michigan. 1. F. cristula, capsule still within calyptra, \times 22. 2. F. foveolata, just prior to capsule dehiscence, \times 22. 3. Either F. cristula or F. foveolata, \times 11; note archegonia (a), antheridia, with associated involucres (b), and juvenile sporophyte and associated pseudoperianth (c).



Fig. 4. Fossombronia cristula from Vincent Lake, with capsules partially enclosed in pseudoperianths and calyptrae.

the lumina are smaller and the muri extend outward unevenly, sometimes as rounded or flattened projections. Evans (1915) noted the similarity in spore ornamentation in the two species but discounted as taxonomically unimportant the small difference in spore size reported by others (35–44 μm in F. cristula vs. 42–50 μm in F. foveolata). Plants of F. cristula and F. foveolata are alike morphologically, and without sporophytes the identification of sterile specimens appears to be impossible.

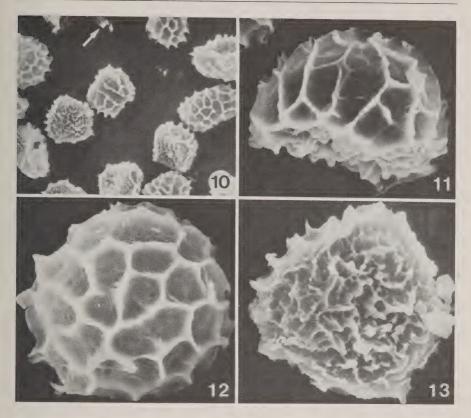
A collection of Fossombronia made by one of us (Crum) at Vincent Lake on 17 October 1976 proved crucial in establishing the presence of F. cristula and F. foveolata in northern Michigan. At the time of collection only one capsule had matured, and it contained elaters of the cristula-type. However, in another preparation a few slender elaters with bispiral thickenings were seen. Because those few elaters were so distinctive (slender, simple, uniform in shape and spiral thickening), it seemed most likely that they were extraneous in origin and not indicative of a range of variation possible in F. cristula. A portion of the collection was shipped live to Miller for further study. When it arrived in Massachusetts on October 21 the plants with their natural substratum were transferred to a glass culture dish and grown at room temperatue in light that passed through a north-facing window. A small amount of distilled water was added whenever the plants appeared dry. The first mature sporophyte (seta elongated, capsule black and irregularly dehiscent) to be produced under those conditions was observed on October 22, and many additional sporophytes matured during the next five weeks. The plants remained vigorous through the winter, although sporophyte production



Figs. 5–9. Fossombronia cristula from Vincent Lake, showing spores and elaters; fig. 9 is a tetrad of spores not yet mature enough to show the surface reticulum.

ceased near the end of November. Of the series of capsules harvested between 25 October and 4 November some contained spores and elaters typical of F. cristula, while others proved to have similar spores but the elaters of F. foveolata. Plants of both species had therefore been growing intermingled at Vincent Lake, a fact that was not apparent from the appearance of the densely packed plants (fig. 4) or from preparations made shortly after the plants were gathered. Our collections from the same place along the shore of Vincent Lake in 1982 contained F. foveolata only.

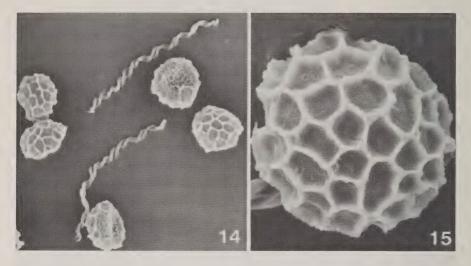
It appears that *Fossombronia cristula* and *F. foveolata* have overlapping times for maturing spores. Both species were in fruit at Vincent Lake on October 17, 1976, and *F. foveolata* was found there with sporophytes again on August 16, 1982. In 1983 *F. foveolata* was collected at Duck Marsh (near



Figs. 10–13. Spores of *Fossombronia cristula* from Vincent Lake. 10. Annular thickening of elater at arrow, \times 350. 13. side view, \times 1380. 12. Distal face, \times 1380. 13. Proximal face, \times 1380.

Lake 16) on October 8. Collections from elsewhere in the Upper Great Lakes region show dates of spore maturity ranging from July 2 through September 29 for this species. The specimen from Kent County in southern Ontario was collected on October 4. The date of the Ontario collection of *F. cristula* was September 11, more than one month earlier than the Vincent Lake collection. We have verified collections of *F. cristula* made in the eastern United States on the following dates: 10 October 1974 (Grassy Pond, Suffolk Co., New York, *G. L. Smith 12*, NYS; grown indoors and spores mature on 8 November), 6 November 1976 (Turtle Pond, Strafford County, New Hampshire, *I. M. Storks s.n.*, NYS; spores mature), and 11 November 1975 (Morgan Bird Sanctuary, Middlesex County, Massachusetts, *N. G. Miller 7936*, NYS; spores mature). Evans (1915) cited specimens of *F. cristula* from Massachusetts, Connecticut, New York, New Jersey, and West Virginia. Of these, the earliest collection with spores was made in September (New York) and the latest was November (Massachusetts and New Jersey).

Plants of Fossombronia foveolata collected in 1982 at Duck Marsh were



Figs. 14–15. Spores and elaters of *Fossombronia foveolata* from Duck Marsh, near Lake 16, Cheboygan County, Michigan (fig. 14, \times 310; fig. 15, \times 1150).

kept in culture throughout the winter, but no new sporophytes were formed. The plants were monoicous. Archegonia and antheridia could be seen in abundance, especially after the plants became somewhat etiolated and clearly showed a 2-ranked leafy organization rather than a seemingly thallose construction. Archegonia were found near the growing tips, and antheridia were scattered somewhat farther back. Both were borne naked on the thallus surface. (A pseudoperianth develops later around the young sporophyte.) The capsules were sessile and immersed (but in the 1983 collection from Duck Marsh, many capsules were exserted on short, stout setae). No evidence of variability of elaters was seen in this or any other Michigan collection of the species.

It seemed a strange coincidence, after years of searching, to find fruiting material of *Fossombronia foveolata* at Duck Marsh the very next day after its collection at Vincent Lake in 1982, yet it was a basic similarity of habitat that prompted the search.

It appears that Fossombronia foveolata grows in the Great Lakes region in open sites, particularly those subject to inundation, especially at lake shores and on river banks, sometimes in the protection of turfy overhangs and also on wet ledges and in crevices of waterfront cliffs, and commonly in association with sedges and rushes and on their decaying remains. At Vincent Lake it grew on wet sand at the shore, in a sparse growth of such plants as Cladium mariscoides, Eriocaulon septangulare, Juncus pelocarpus, Hypericum majus, Viola pallens, and Lycopodium inundatum. In that same habitat was Sphagnum subsecundum, which is generally indicative of somewhat minerotrophic conditions. At the outer margin of Duck Marsh, it was found on moist sand of little organic content at the bottom of a shallow firebreak ditch in association with Agrostis hyemalis var. tenuis and Viola lanceolata.

The second collection at Duck Marsh was made in a wetter part of the marsh on black organic sand around the bases of *Chamaedaphne calyculata* and in close association with *Juncus militaris* (and other species of *Juncus*), *Hypericum virginicum* (and *H. boreale* or *H. ellipticum*), *Eriocaulon septangulare*, *Polygonum amphibium*, *Lycopus americanus*, *Carex viridula*, *Drosera rotundifolia*, and *D. intermedia*. The ephemeral pygmy moss *Ephemerum crassinervium* was also found on the mucky black soil. It is also rare in northern Michigan. (*Juncus militaris* is known from only a few Michigan localities.)

The following Michigan specimens were examined. All are in the Herbarium of the University of Michigan unless otherwise noted.

Fossombronia foveolata Lindb.

ALGER CO., in cracks of calcareous sandstone cliffs over Lake Superior, Au Train Bay, W. C. Steere, Sept. 6, 1936; in crevices of rocks facing Lake Superior, Au Train, W. C. Steere 522, July 1933. CHEBOYGAN CO., in small patches on bare spots of thin, wet humus over sand near lake margin, Vincent Lake, H. Crum, 17 October 1976 (NYS), on moist, sandy shore of Vincent Lake, in the open, H. Crum & N. G. Miller, Aug. 16, 1982; on moist sand at the bottom of a shallow firebreak ditch, at the open (outer) edge of Duck Marsh (north of Lake 16), near Duck Lake Road, Sec. 8, T37, R1E, H. Crum, Aug. 17, 1982; around bases of Chamaedaphne on wet humic sand in the Juncus militaris (inner zone) of Duck Marsh, M. Penskar, Oct. 8, 1983. MARQUETTE CO., over moist, sandy soil among rushes, edge of Deer Lake, R. M. Schuster 17060, July 20, 1949 [possibly from nearby Baraga Co.]. ONTONAGON CO., on wet ground, shore of Carp Lake, Porcupine Mountains, H. T. Darlington 133, 138, Aug. 22, 1923. PRESQUE ISLE CO., on wet, porous soil, base of grass and sedges, Big Lake, L. F. Koch 2976, Aug. 2, 1948.

Fossombronia cristula Aust.

CHEBOYGAN CO., in small patches on bare spots of thin, wet humus over sand near lake margin, Vincent Lake, *H. Crum*, Oct. 17, 1976.

We are grateful to Anton Reznicek for determining the plants growing with *Fossombronia* at Vincent Lake and the firebreak at Duck Marsh. Michael Penskar provided information on plants associated with his specimen collected at Duck Marsh. David Bay and Jeffrey Holcombe made the photographs, and Joseph Rohrer and Umesh Banerjee took the SEM pictures.—Published in part as New York State Science Service Journal Series No. 432.

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REVIEW

NORTH AMERICAN TERRESTRIAL ORCHIDS, Symposium II, Proceedings and Lectures. Ed. Elmer H. Plaxton. 1983 Michigan Orchid Society. vii + 143 pp. Available from Michigan Orchid Society, c/o Raymond McCullough, 14800 Harrison Ave., Livonia, MI 48154. \$17.95 postpaid (+4% sales tax for Michigan residents).

This book presents proceedings from the October 1981 American Orchid Society and Mid-America Congress meetings held at Southfield, Michigan. It covers many facets of North American terrestrial Orchid biology, including artificial seed germination, culture, and aspects of distribution, ecology, and taxonomy in Canada, Mexico, and the United States, as well as protected habitats in Michigan, fluctuations in populations in the Great Lakes region, and fragrance in flowers. An article on orchids in the Boundary Waters Canoe Area of northern Minnesota, presented at the symposium, was published in *Orchid Digest* for Nov.–Dec. 1982, is reprinted here without re-pagination, resulting in pages 65–80 being numbered 213–228. Twelve pages of color photographs are an attractive feature of the volume.

The articles on seedlings and seed germination provide much information, as well as recipes for media that the adventurous can try. The article on *Cypripedum* culture provides useful information on soil mixes, dividing plants, pH preferences, etc. Students of the North American flora will be surprised that there is a good deal still poorly understood in the taxonomy of native terrestrial orchids. The Yellow Lady's-slipper complex is a good example, as are certain species or species complexes within *Corallorhiza*, *Malaxis*, and *Platanthera*. Much also remains unknown about the autecology and pollination biology, floral fragrances is a direction for further research. Preservation of orchid populations and habitats is another important issue. It is also not a simple matter, as attested to by the observations of fluctuations in orchid populations and the variability in the lifespans of native terrestrial orchids.

Errors, typographical or otherwise, are few and not of great consequence. The two photographs of *Spiranthes romanzoffiana* (pg. 67 (215)), however, surely represent *S. cernua*. At \$17.95 per copy, the book is not too expensive, considering the color plates. It is a worthwhile addition to any orchidophile's library.

—A. A. Reznicek.

SOME SPECIES MERGERS AND NEW COMBINATIONS IN THE OHIO FLORA

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In assembling a taxonomy for some 800 species of the families "Linaceae through Campanulaceae" to be covered in a forthcoming volume of the Ohio Flora series, mergers of four species-pairs are necessary in order to achieve a workable and consistent taxonomy. In reaching these decisions, specimens were examined from throughout the ranges of the taxa in question, but especially from Ohio. In each of the four instances, intergradation is so extensive that continued separation at the species level is illogical. In each instance there exists one of the several types of sympatry characteristic of geographic varieties.

In the fifth situation covered, a name is provided for a well known form from eastern United States.

1. (Euphorbiaceae) **Acalypha virginica** L. var. **rhomboidea** (Raf.) Cooperrider comb. et stat. nov. Basionym: *Acalypha rhomboidea* C. S. Rafinesque. New Flora and Botany of North America. Part 1:45 (1836). Three-seeded Mercury.

All characteristics used to separate A. virginica var. virginica from var. rhomboidea: shape of blade, petiole-blade length ratio, number of lobes and depths of sinuses of pistillate bracts, and types of stem and bract pubescence intergrade and occur in every combination. While fostering the separation of the species in this group, which had long been combined, Weatherby (1927) nevertheless aptly noted that the taxa are "separated by characters no one of which is constant." In my experience this is understating the situation. Without a single reliable diagnostic character or combination of characters, one is reduced to assigning identification of each specimen on the basis of a majority count of character states. Even this is made more difficult because of the intergradation between character states.

Miller (1964), who treats the two as distinct species, notes that the two have "much the same range." Her distribution maps show A. rhomboidea to be the more frequent member of the pair in states along the eastern coast of the United States, but show also that it reaches as far west as Texas, Oklahoma, Kansas, and Nebraska. Acalypha virginica is the more frequent taxon west of the Mississippi River, with a western boundary almost identical to that of A. rhomboidea, but it extends east as far as New Jersey, Maryland, and the Carolinas. In short, their ranges show one type of pattern found in conspecific geographic varieties.

A third Ohio taxon, A. virginica var. deamii Weatherby, is best treated

at that rank. It has been treated at the rank of species by Miller (1964) and Webster (1967), but on the other hand merged without rank of any kind under *A. rhomboidea* by Gleason & Cronquist (1963).

Miller (1964) reports chromosome counts of n = 20 for var. *virginica* and var. *deamii*, and notes an earlier report of n = 21 for var. *rhomboidea*, making it likely that the three varieties are homoploid.

2. (Boraginaceae) **Cynoglossum virginianum** L. var. **boreale** (Fern.) Cooperrider comb. et stat. nov. Basionym: *Cynoglossum boreale* M. L. Fernald. Rhodora 7: 250 (1905). Wild Comfrey.

Fernald (1950) uses four key characters to separate *C. virginianum* from *C. boreale:* width of larger leaves, calyx length, corolla breadth, and nutlet length. Although he presents an overlap in the variation in only the first character and discrete ranges of variation in the last three, it has been my experience that there is in fact extensive intergradation in all four characters, such that many specimens cannot be satisfactorily assigned to either species. Johnston (1924), while accepting *C. boreale* at the rank of species, noted that others had merged it without rank under *C. virginianum*, and wrote, "surely it is deserving of varietal rank at the very least." In my judgment it is a geographic variety. There is considerable overlap in the ranges of the two taxa (Fernald, 1950), with var. *boreale* occupying the northern part of the species' range, and var. *virginianum* the southern part.

I have found no chromosome number reports for either taxon.

3. (Labiatae) **Monarda fistulosa** L. var. **clinopodia** (L.) Cooperrider comb. et stat. nov. Basionym: *Monarda clinopodia* C. Linnaeus. Species Plantarum, vol. 1:22 (1753). Wild Bergamot.

The diagnostic characters used to distinguish var. *fistulosa* from var. *clinopodia:* differences in the amount of pubescence and in the color of the corolla, intergrade in a continuum of variation. The distribution maps of McClintock & Epling (1942), show the range of *M. clinopodia* to lie wholly within the range of the more widespread *M. fistulosa*. This is yet another pattern of distribution associated with geographic varieties, var. *fistulosa* being found throughout the species range, var. *clinopodia* limited to the eastern part.

Scora (1967) reports chromosome counts for both taxa as "n = 18 or approximately that number."

 $Monarda \times media$ Willd. was shown by Scora (1967) to be an interspecific hybrid, one of whose parents is certainly M. didyma L. Lending indirect support for treating var. fistulosa and var. clinopodia as conspecific is Scora's conclusion that the other parent of M. \times media could be either M. fistulosa or M. clinopodia. The classification adopted here has the incidental advantage of making that point moot.

4. (Labiatae) **Pycnanthemum verticillatum** (Michx.) Pers. var. **pilosum** (Nutt.) Cooperrider comb. et stat. nov. Basionym: *Pycnanthemum pilosum*

T. Nuttall. The Genera of North American Plants, vol. 2:33 (1818). Mountain Mint.

The main diagnostic feature separating var. *verticillatum* from var. *pilosum* is variation in the amounts of pubescence of several parts of the plant body. I have found a pattern of continuous variation between the extremes. Other key features sometimes used to separate the two, aspects of the inflorescence and the bracts, are qualified by "often" or "usually," reflecting their inconstancy and lack of reliability as diagnostic features.

The distribution maps of Grant & Epling (1943) show a region of sympatry between the more eastern var. *verticillatum* and the more western var. *pilosum*, a geographic varietal distribution pattern similar to that noted earlier in *Cynoglossum virginianum*.

The two taxa have been combined previously, but under the generic name *Koellia*. Using the same epithets as above, Kuntze (1891) published the combination *Koellia verticillata* (Michx.) Kuntze var. *pilosa* (Nutt.) Kuntze.

Chambers (1961) reports 2n = c.76-78 for *P. verticillatum*; Chambers & Chambers (1971) report 2n = 78 for *P. pilosum*, suggesting that the two are homoploid.

5. (Violaceae) **Viola sororia** Willd. forma **priceana** (Pollard) Cooperrider comb. et stat. nov. Basionym: *Viola priceana* C. L. Pollard. Proc. Biol. Soc. Wash. 16:127 (1903). Confederate Violet.

Since Pollard (1903) first described this taxon at the rank of species, it has been treated in a number of ways. Gleason & Cronquist (1963) call it *V. papilionacea* Pursh var. *priceana* (Pollard) Alexander. Without a name at the rank of form, it has nevertheless been referred to as a form of *V. papilionacea* by Rickett (1967), and as a form of *V. sororia* Willd. in Hortus Third (Staff of the Liberty Hyde Bailey Hortorium, 1976). Fernald (1950) incorrectly equated it with *V. papilionacea* forma *albiflora* Grover. Both forms occur in Ohio and are clearly distinct. Grover (1939) described forma *albiflora* as having "petals wholly white or with the lowest one streaked with purple." Pollard (1903) had earlier correctly described *V. priceana* as having petals "pale lilac, shaded with purple near the base . . . and conspicuously purpleveined."

Russell (1965) in a classification that has been widely adopted merged *V. papilionacea* under *V. sororia*. When this is done, the white-flowered form described by Grover is correctly called *V. sororia* forma *beckwithae* House, a name published in 1923. A name for Pollard's form, within *V. sororia*, is published above. Since the sole diagnostic feature is the distinct corolla color, and since the plant occurs sporadically and unpredictably in nature, the rank of form is the most appropriate for this plant. It is, however, unusual in being a geographically restricted form found in addition to its sites in Ohio, in Kentucky, Arkansas, North Carolina, and Georgia (Gleason & Cronquist, 1963).

I thank Dr. Edward G. Voss for a critical reading of the manuscript, and I acknowledge with thanks support from the Ohio Department of Natural Resources that made this work possible.

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DO SAND DUNES HAVE SEED BANKS?

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Much research has been conducted in recent years on various aspects of permanent seed banks in an attempt to understand their ecological and evolutionary role. Seed banks have been described from forests, grasslands, arable fields, and wetlands. From these studies have come many explanations for the existence of seed banks and their significance. There have also been studies (Thompson & Grime 1979, Livingston & Allessio 1968, Donelan & Thompson 1980, Oosting & Humphreys 1940) that compare seed banks of different habitats. These studies have primarily focused on testing the theory that seed banks reflect the vegetation of past successional stages. The literature on seed banks seems well developed with many theories and postulations which should prove useful in forecasting the attributes of a seed bank in an as yet unstudied habitat.

The east shore of Lake Michigan consists of dunes that grade from bare sand at the lake's edge inland over dune ridges to stabilized forested dunes. The seed bank of this type of habitat has not been studied. This habitat thus provides a unique opportunity to synthesize the ideas on seed banks to predict features of the dune's seed bank. The dunes also offer an opportunity for comparative work on successional stages.

REVIEW OF CURRENT THINKING

We have organized the literature on seed banks into three artificial categories based on the development of the seed bank: (1) the variables influencing seed arrival at the site, (2) the variables influencing seed penetration into the soil and (3) the variables influencing seed persistence in the soil to become part of the permanent seed bank.

Seed arrival at the site. Local vegetation would appear to be the logical source for most seeds in the seed bank, yet studies (Thompson & Grime 1979, Oosting & Humphreys 1940) have shown that this may not always be the source of the seeds. Of course, seeds may also be blown into an area or carried in by animals, rivers, or other means. Kellman (1974), however, found seed dispersal across vegetation boundaries to be minor, particularly in woody habitats. Rabinowitz (1981) found no close association between the seed bank and seed rain, where seed rain included all seeds falling on the soil, whether from the local vegetation or from an outside source. The suggestion is that if seeds currently falling on the soil are not represented in

the seed bank, then possibly seeds remain in the seed bank from past successional stages (Livingston & Allessio 1968, Oosting & Humphreys 1940, Olmsted & Curtis 1947, Donelan & Thompson 1980), and that the size of the seed bank probably decreases in the more advanced successional stages. In summary, these studies suggest that the seeds in a seed bank may arrive from the successional past, the current cover vegetation, outside vegetation, or combinations of these.

Seeds entering the soil. Seed of the current or historic seed rain need not only land on the site but also enter the soil to become part of the permanent seed bank. This presents some physical problems that may provide insights into seed banks. Burial can certainly be expedited by disturbance of the soil. The arable field studies show exceptionally large seed banks, and Donelan & Thompson (1980) related the large seed banks of early successional stages to the fact that early stages are often associated with large-scale disturbance. Disturbance of a more restricted nature can be caused by burrowing animals that also open the soil for seeds. Perhaps another important consideration is the size of the seeds. Smaller seeds more easily filter into the soil than larger ones, and smaller seeds are more common in seed banks. Lastly, in the absence of major disturbance, the characteristics of the soil surface may determine the underlying seed bank. In forests, where seed banks poorly reflect the local vegetation, it is suggested that heavy forest litter may provide an impenetrable surface.

Persistence once buried. A buried seed does not necessarily enter the permanent seed bank. It may quickly germinate or rot or be otherwise destroyed. Why do some seeds persist in the seed bank? Physiological factors determine persistence, but for this study ecological or evolutionary reasons for persistence are more relevant. Perhaps the best predictor of seed persistence is the length of the plant's life history. Annuals tend to have seeds of greatest longevity, herbaceous perennials with no vegetative reproduction have medium longevity, and herbaceous perennials with vegetative cloning have seeds of least longevity (Werner 1979). Perennials, particularly those with vegetative reproduction, have a reliable method of transporting genetic material through time without seeds. Therefore, the need for a seed bank might be much reduced. Annuals, on the other hand, can be destroyed by one adverse season. A seed bank can provide a dormant link with the future and by representing seeds from many past seasons preserve genetic variability (Templeton & Levin 1979). However, in a study of grasslands dominated by annual grasses, Young et al. (1981) found a surprising lack of residual germinable seed.

The seeds of herbaceous species seem to persist more than woody species. Again it may be reflection of adult longevity or the fact that woody plant seeds tend to be energy-rich and thus the target of predators.

EXPECTED RESULTS

The seed bank literature seems complete enough to suggest that it is possible to predict the presence and abundance of a seed bank of a new habitat. This was attempted for a Michigan sand dune. The Michigan dunes originate at the shore as bare sand deposited by wind and water action. This beach area, or strand, has no ecological past; it is bare of local vegetation, and since winds are from the west across Lake Michigan, it is unlikely that they carry seeds. The only potential vectors for seeds would be birds and other animals, water, and any rare offshore breezes. With such limited supply of seeds it was expected that there would be no seed bank under the strand.

The next zone of vegetation inland consists of the beach grasses, perennials which require shifting sand for survival. The shifting sand would allow opportunities for seeds to be buried in the soil but at the same time provide constant re-exposure of seeds once buried. This constant turmoil of the sand might not allow an opportunity for a seed bank to develop. At the same time, since the local vegetation is perennial, it may not be contributing to the seed bank anyway. In fact, Maun (1981), in a study of one of these grasses, *Calamovilfa longifolia*, found that seeds buried less than six cm germinate in the fall after release and survive while those buried more than seven cm also germinate but fail to reach the surface. Therefore, because of the long-lived nature of the local vegetation, the lack of a successional past containing vegetation, and continual disturbance providing current germination opportunities for seeds present, it seems unlikely that a seed bank would exist under the beach grass zone of vegetation.

Inland from the first few grass-covered ridges are the panne and beach pools which are usually blown out areas where the water table is exposed, resulting in year-round pools. In this area the variety of vegetation is greater. The vegetation includes *Juncus* spp., which is one of the known producers of seed banks. Therefore, the local vegetation now provides a likely source of suitable seeds. Also these blown-out areas are depressions which might be expected to be collection basins for wind blown seeds. It is not expected that the earlier successional stages would provide any seeds. The soil surface is still loose sand, and so seeds should have an opportunity to enter the soil. Therefore, it is here that we expect the first seed bank in the successional series.

Lastly, the dunes are stabilized by woods. Most studies indicate that the seeds of the trees are unlikely to enter the soil. However, we would expect the woods to draw more seed-eating birds than any of the previous habitats, and so we would expect seeds to be transported in from outside habitats. Yet from Kellman's studies (1974), we would not expect this to be a significant factor. The soil surface in the woods is stabilized by a litter layer which may make it difficult for bird transported seeds to enter the bank. We might expect the bank in the woods to reflect the seeds remaining from the beach pool; however, this is problematic because the level of the beach pool is at water table while the dune woods are on top of dunes. Any seeds remaining from



Fig. 1A. Seed bank study area, Lake Michigan sand dunes, Saugatuck, Michigan. Beach strand.

beach pool days might be buried at a considerable depth (tens of feet). Also, the woods is the most advanced successional stage; this, according to Donelan (1980), suggests a reduced seed bank. Therefore, we would expect some seed bank based on bird- and other animal-transport, perhaps some from the current herb layer and, as a remote possibility, seeds remaining from beach pool days.

METHODS AND MATERIALS

The study site is a relatively undisturbed, privately owned, dune area along Lake Michigan just north of the mouth of the Kalamazoo River, in Allegan County, Saugatuck Twp. (T3N, R16W N.½ of Sect. 4) immediately south of Saugatuck State Park. The site consists of a gently sloping strand (Fig. 1A) extending away from the lake for approximately 100 feet to low foredunes rising approximately 8 feet above the beach. The gently undulating foredunes (Fig. 1B) extend approximately 100 yards to a lower panne (Fig. 1C) with scattered beach pools. Behind the panne (eastward from the lake) are higher, stabilized, forested dunes (Fig. 1D) interspersed with blowouts.

The beach vegetation consists entirely of *Cakile edentula* (Sea Rocket) with some *Ammophila breviligulata* (Marram grass) on the higher portions close to the base of the foredunes. The foredunes are dominated by



Fig. 1B. Foredune (junior author collecting sample).



Fig. 1C. Panne with forest and blowout in background.



Fig. 1D. Dune forest with foredune in foreground.

Ammophila breviligulata and Calamovilfa longifolia (Sand Reed grass) with scattered Populus deltoides (Cottonwood) trees up to 15 or 20 feet tall. Other plants scattered throughout the foredune include Artemisia campestris (Wormwood), Lithospermum carolinense (Hoary Puccoon), Toxicodendron rydbergii (Poison Ivy), Euphorbia polygonifolia (Seaside Spurge), Cirsium pitcheri (Pitcher's Thistle), Hypericum kalmii (Kalm's St. Johns Wort), Arctostaphylos uva-ursi (Bear Berry), Hudsonia tomentosa (False Heather). The panne vegetation is dominated by grasses, sedges, and rushes, Salix spp., and Pinus banksiana. The young dune forest sampled is dominated by Acer saccharum (Sugar Maple), Sassafras albidum (Sassafras), and Tsuga canadensis (Hemlock). No attempt was made to identify ground cover species owing to the lateness of the season.

On November 23, 1981, soil samples were collected from each of four habitats, 20 from the beach, foredune, and dune forest, and 19 from the panne (due to sampling error). Samples were collected along a 100-ft. transect formed by a glass fiber tape; points along the transect were selected from a random numbers table and translated into foot increments of the tape. The sampling device was a length of 3 in. I.D. P.V.C. 1120 thin-wall pipe pressed into the sand to a depth of 4.5 in. (determined by a line drawn around the outside of the pipe). The surface duff was scraped away before sampling in order to sample the permanent seed bank as opposed to surface seeds recently released. The samples were placed in Zip-Loc plastic bags, sealed and labeled.

In the laboratory, the samples were removed from the bags, spread in plastic growing flats to a depth of approximately one inch, and placed in a well-lighted room. The sample flats were arranged on tables in an interspersed manner so that those from the beach, foredunes, panne, and dune forest were not all together to prevent growing conditions from favoring one zone over another. Two control flats of greenhouse sand were included to detect any seed contamination from the laboratory. The flats were watered daily or as needed and examined weekly for six weeks for evidence of germination. This phase of the experiment was terminated on January 3. 1982. At that time the samples from all areas except the panne were allowed to dry out, but the latter were each placed in larger containers of water so that the samples were flooded for a period of 10 days in the event that any of the seeds present would need flooding in order to germinate. Then the panne samples were allowed to dry out slowly and watered as needed for an additional four weeks. After thorough drying, all the samples were sifted through two grades of soil sieves, 0.35 cm and then 0.1 cm (the smaller sieve size was the size through which the sand particles would go but anything larger would be retained). The debris was examined through a dissecting microscope for any seeds, which were removed, stored in coin envelopes at room temperature, and tetrazolium tested for viability. No attempt was made to identify the seeds before the viability tests; the seeds were destroyed by the testing.

RESULTS

No seeds germinated in any of the samples from any of the four zones or in the controls. After six weeks, when it was apparent that no seeds were going to germinate, we decided to (1) submerge the samples from the panne in water for a period of time to see if that would stimulate any germination since much of that zone has standing water forming beach pools, and some seeds might germinate only in saturated conditions, and (2) to sift all the samples to see if any seeds were present.

Figure 2 displays the number of seeds found in the samples. It is interesting to note that no seeds at all were found in either the beach or foredunes and very few seeds in the panne (X = 0.74 per sample) and forest (X = 3.2 per sample), although in a few of the foredune, virtually all of the panne, and most of the forest samples there were a number of broken seed fragments. None of the seeds found in any of the samples tested positive for viability.

DISCUSSION

Our results fairly closely match the expected results. Both the beach and foredune areas had no seed bank. The panne did have seeds, although perhaps not the large numbers that might have been expected and of question-

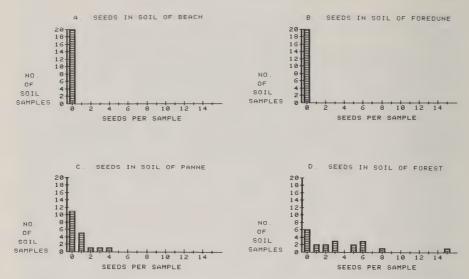


Fig. 2. Number of seeds in soil samples from Lake Michigan sand dunes, Saugatuck, Michigan.

able viability. Most surprising was the forest, where the largest numbers of seeds were found. The large increase from the panne suggests that either the forest has a significant source of seed not available to the panne or the stability of the forest limits the opportunity for the seeds to leave the seed bank once entrapped. Although the latter may not be the explanation, it seems worthy of consideration. The literature suggests that disturbance increases the size of the seed bank, but such studies were done on arable land with a regular and intermittent disturbance difficult to envision in nature. It seems reasonable that annual plowing would increase the seed bank by allowing soil entry. However, in the beach system, the disturbance is not intermittent. This constancy may work against a seed bank. The seeds may be buried too deeply ever to resurface, or they may resurface very quickly and germinate, or the physical action of the blowing sand may destroy them before they can enter the bank.

SUMMARY

The seed bank of an east-shore Lake Michigan dune area including beach, foredune, panne, and dune forest near Saugatuck, Michigan, was studied. A review of seed bank studies is presented together with a prediction that little or no seed bank will be found in the dune area. The study supports the prediction. No seed bank was found in any of the areas tested; in fact, very few seeds were found.

ACKNOWLEDGMENTS

We wish to thank Sally Speaker, Michelle Hohn, and Leonard Bierwith for assistance in the project.

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ADDITIONS TO THE PTERIDOPHYTE FLORA OF MARQUETTE COUNTY, MICHIGAN

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The pteridophyte flora of Marquette County was examined in detail by Hagenah (1963). His listing is wonderfully complete considering the limited time he had for field work in the area. This is probably due to his understanding that the great Precambrian rock shield is not as monolithic as many people believe. There are limestone formations within the shield complex, although they are much altered and do not resemble limestone to the typical observer. These metamorphic rock complexes are still chemically intact enough to provide a home for many lime-loving ferns that otherwise could not survive in the area.

Three miles east of the area Hagenah explored, the Kona formation creates a complex of cliffs and low outcrops consisting of altered dolomite characterized in most places by irregular bands of silica. The bands are remains of ancient algal structures and are among the oldest non-microscopic fossils known. Since these silica bands protrude a centimeter or so from the softer lime they often provide a foot-hold for plants. Among the plants clinging to these rock faces is *Asplenium viride* (Green Spleenwort). The closest reported stations are nearly 200 miles away in Chippewa County. Near Bushell Lake about 100 of these plants cover one north-facing cliff in company with a few plants of *Cystopteris fragilis* (Fragile Fern). Farther west along the strike of the same rock formation an occasional plant can be found but no more than one or two at a location. These more solitary plants have more varied companions: one cliff has *Asplenium viride*, *A. trichomanes*, *Cryptogramma stelleri*, *Polystichum braunii*, *Dryopteris intermedia*, and *D. marginalis* along 10 meters of rock face.

Hagenah was unable to substantiate an early report of *Thelypteris novaboracensis* (New York Fern) in the area and noted that the nearest known station is more than 100 miles to the east. However, small numbers grow near Abrams Lake in Skandia about 20 miles south of the location of the old report. The fern can be easily overlooked as it grows hidden among *Athyrium thelypterioides* (Silvery Glade Fern); both species grow to be about 4 dm in height hereabout. Hagenah also could not verify the local occurrence of *Equisetum variegatum* (Variegated Horse-tail). He identified the collection on which the report was based as E. × nelsoni. However the true *E. variegatum* does grow in a couple of locations south of the city of Marquette.

Specimens of all the species mentioned above are preserved at Northern Michigan University.

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NOTICE

With this issue of *The Michigan Botanist* Nancy and I begin our tenure as co-editors. We wish to thank the Board of Directors of the Michigan Botanical Club for their confidence in appointing us. We will endeavor to work to the high standards of the previous editors, Drs. Voss and Crum. *The Michigan Botanist* is a publication of which the members of the Michigan Botanical Club can be proud.

At this time we encourage submission of manuscripts on the plants of Michigan and the Great Lakes region. All submissions will be given careful consideration by the editors and reviewers. Articles of an educational nature are encouraged, as well as those of a more scientific orientation. We want the journal to be something members, both scientific and amateur, will look forward to receiving.

The stock of photographs suitable for use on the cover is down. We need black and white photographs with a horizontal format of various plants, habitats, and botanical activities. The plants, places, and people should be identified, and the photographer's name included for each photograph.

We would appreciate authors following a few simple guidelines when submitting manuscripts for publication. Please type the manuscript using double-spacing throughout with at least 1 inch margins. A clear clean manuscript will go a long way toward reducing misinterpretation. In addition, we need room at the margins of the manuscript to make notes to the printer. If a word processor is used, do not justify the right hand margin. Submit two complete copies of the manuscript. One copy will be sent out for review by a person knowledgeable in the subject of the paper. The other is used by the editor for preliminary editing. Send one set of original drawings or clear photographs for all figures and plates. Copying machines, even those from the leading manufacturers, do not make clear enough copies for reproduction in the journal. In addition, please do not send the figures or plates in bits and pieces expecting the editors to do the final set up. It costs money and time to have someone put figures together. Furthermore, we might not do the way you want it done. Do not integrate the tables, figures, and plates into the text. Text, tables, and figures are set up separately by the printer and integrating them will cause difficulty in production. Arrange the parts of the manuscript in the following order: title page, text, literature cited, tables, figure legends, and figures. Read the proof for typographic errors and return it promptly. If the proof is not returned promptly, we will correct those errors we find and go ahead with publication. Do not make major corrections at this time. It costs money to make these changes, so the fewer we make the less our cost. Following these guidelines will help us in the production of a quality journal.

We are looking forward to working on *The Michigan Botanist* and to receiving interesting papers on the plants of Michigan and the Great Lakes area.

JIM and NANCY WEBER

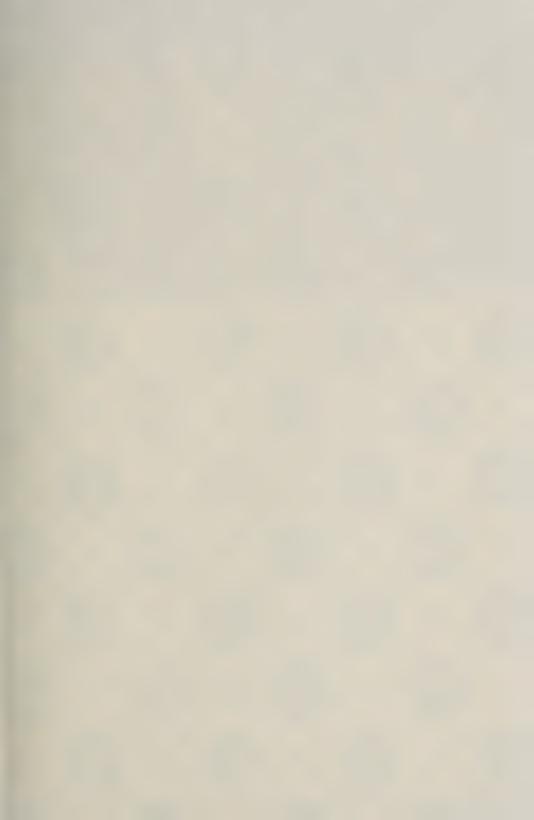


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Legend Less than 1 mature tree per acre, dominated by prairie grasses and forbs. PRAIRIE* Between 1 and 15 trees per acre, nearly pure bur pak. BUR OAK OPENING OAK SAVANNA More than 15 trees per acre; composition similar to oak savanna but with slightly less yellow and black oak and the addition of small amounts of red oak. OAK FOREST Areas dominated by white pine, with small numbers of white and black oak. PINE FOREST OAK-PINE FOREST BEECH-SUGAR MAPLE FOREST Beech, hemlock, and sugar maple with small amounts of basswood, yellow birch, white pine, elm (American and slippery), white ash and ironwood. NORTHERN CONIFEROUS-HARDWOOD FOREST SOUTHERN FLOODPLAIN FOREST SOUTHERN SWAMP Vetlands dominated by tamarack. TAMARACK SWAMP SPRUCE SWAMP Wetlands dominated by black ash BLACK ASH SWAMP CEDAR SWAMP Wetlands dominated by white pine PINE SWAMP Wetlands dominated by hemlock. HEMLOCK SWAMP NORTHERN MIXED SWAMP FOREST SHRUB-CARR ALDER THICKET WET PRAIRIE

* Numbers identify prairie locations. See opposite side for prairie names.

MARSH

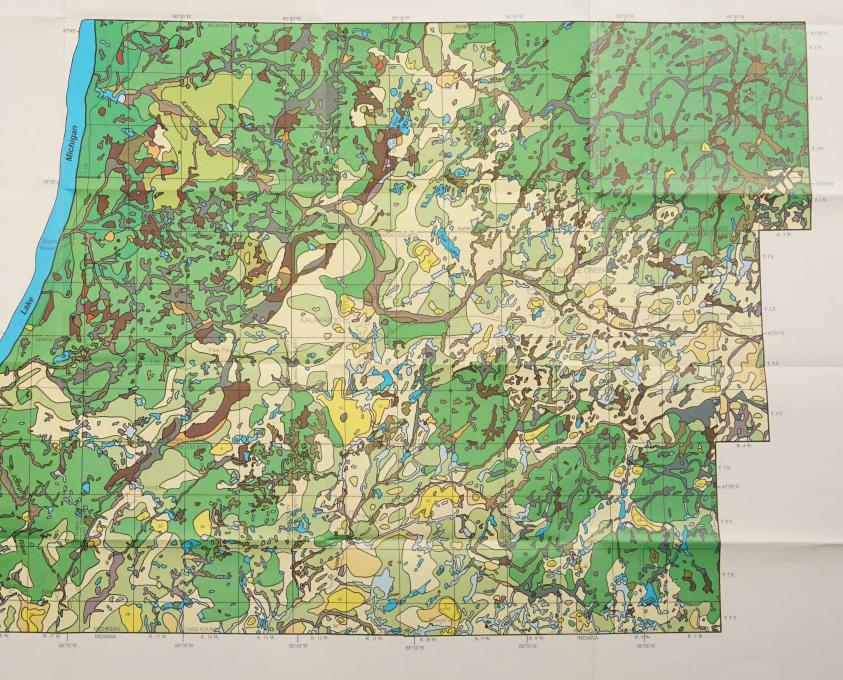
UNDIFFERENTIATED WETLAND

The areas designated "marsh" by the surveyors probably included cattail and bulrush marshes, fens, open bog mats, and also some of the wetter sedge meadows.

County Names 1. Allegan 2. Burry 3. Eator 4. Van Buren 5. Kalamazoo 6. Calloun 7. Bernen 1. [2] 1. [2] 6. Cass

Presettlement Vegetation of Southwestern Michigan

By
Lawrence G. Brewer, Thomas W. Hodler and
Henry A. Raup
Western Michigan University



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Presettlement Vegetation of Southwestern Michigan

Lawrence G. Brewer, Thomas W. Hodler and Henry A. Raup

Western Michigan University

DELINEATION OF VEGETATION BOUNDARIES. A number of techniques were used to delineate the boundaries between different vegetative communities. For utilized forcest types the migrate part of the part o

delimitated boundaries were identified at the looporaphic map scales of 124,000 and 1582,500, respectively, and compiled rice 125,000 mosaci as depicted on the reverse side. Boundary line accuracies are determined at the larger scale topographic maps.

In Michigan, the land parsets were defined using the U.S. Rectangular Survey System (township and range). Generally the separate surveying crees worked System (township and range). Generally the separate surveying crees worked System (township bearing completed in one to three weeks.

Although a description of the vegetation vision that the other suddwide the interior time square risk sections. Surveying was done throughout the year, with an average township bearing completed in one to three weeks.

Although a description of the vegetation was not the surveyor's main objective, they were required to gather specific vegetation information. This information included two vitriess trees at each section corner; two bearing trees hallway between such corners; two additional bearing sections of the vegetation was not the surveyor's main objective, they were required to gather specific vegetation information. This information included two vitriess trees at each section corner; two bearing trees hallway between such corners; two additional bearing sections of the control of the co

categories can be considered accurate only to $\pm lambda$ mile. Boundary lines between mesic and dry forest can be considered accurate to $\pm lambda$ mile.

Information used in determining boundaries for the lowland forests (Southern Floodplain Forest, Southern Swamp Forest, and the various Northern Swamp Forests) included the surveyor's descriptions of entering and leaving swamps or bottomlands, the individual witness and line trees, the Ising of trees at the end of each mile, and the control lines on topographic maps, in nearly all foreward forests there was at least one survey line describing the points where surveyors entered or left these forests, in most cases these points concided with a distinct decrease in eliavation. For following the contiour lines where surveyors entered and left a swamp or thooglain it was possible to unline lowland forests where there were no escorol lines available.

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Thanks go to Dr. Richard Brewer for his work on the classification system and rules for drawing boundaries on the Kalamazoo Courtly map (Hodier, et al., 1891) which was prototype for his map. Lacke Cork and Provity Hepper helped assemble the data for Allegan and Barry Counties. Km Chapman, Gerard Donnelly, 961 Ebbers, David Mahan, and Wallam Rose read the mauscript and give helpful comments.

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1194.5. Forest associations of Ottowa County, Michigan, at the time of original survey. Pap. Mich. Acad. Sci. 28:47-50.

PRAIRIE NAMES

ALLEGAN COUNTY

BARRY COUNTY 1 Bull's Prairie 2 Garden Prairie* 3 Scale's Prairie*

EATON COUNTY 4 Charlotte Prairie

VAN BUREN COUNTY 5 Little Prairie Ronde

toland's Prairie
CALHOUN COUNTY
16 Cook's Prairie
17 Dry Prairie
18 Goguac Prairie
19 McCamly Prairie
20 Wilder's Prairie
21 Prairie with no name
22 Prairie with no name
23 Prairie with no name

BERRIEN COUNTY 24 Portage Prairie 25 Terre Coupe Prairie 26 Wolf's Prairie

35 roungs Frairle
ST. JOSEPH COUNTY
36 Dry Prairle
37 Goodrich Prairle
38 Indian Prairle
39 Johnnycake Prairle
40 Nattawa Prairle
41 Sturgis Prairle
42 White Pigeon Prairle

Supplement to The Michigan Botanist. Volume 23, Number 4, October 1984.





